TAXONOMY AND DISTRIBUTION OF *GENTIANA* (GENTIANACEAE) IN MEXICO AND CENTRAL AMERICA. I. SECT. *PNEUMONANTHE*[1]

JAMES S. PRINGLE
Royal Botanical Gardens, Hamilton, Ontario, Canada

This paper is the first of two that together will constitute a taxonomic monograph on *Gentiana* L. in Mexico and Central America. No such monograph has previously been published, nor does any modern floristic work provide for identification of all these species.

Following Gilg's (1895) treatment of the Gentianaceae, as modified by Wagenitz (1964), *Gentiana* is included in the tribe Gentianeae, subtribe Gentianinae. Tribal and subtribal traits have been given by these authors.

The circumscription of *Gentiana* accepted here follows that in publications on the Gentianaceae by Smith (1936; 1967), Fabris (1960), Gillett (1963), Toyokuni (1963), Mason & Iltis (1966), Nilsson (1967), Tutin (1972), and Weaver & Rüdenberg (1975). As thus delimited, *Gentiana* is distinguished from other genera in the Gentianinae by the following combination of characters: calcium oxalate crystals in the leaves (except in sect. *Calathianae* Froel.); a continuous intracalycular membrane (except in at least part of sect. *Chondrophyllae* Bunge); three primary veins per petal; appendages, or plicae (discussed below), between the primary divisions of the corolla (except in *G. lutea* L.); basifixed anthers; naked nectar-secreting glands borne on the gynophore; septicidal, capsular fruits; no fringes, scales, or nectaries on the interior surface of the corolla; and no marginal fringes on the corolla lobes. This circumscription of *Gentiana* is narrower than that in most North American floras in that it excludes those North American species included by Gillett (1957) in *Gentianella* Moench. It is, however, more inclusive than that of Löve & Löve (1975), who restricted *Gentiana* to the five European species treated by Tutin (1972) as sect. *Gentiana*. In this restricted generic concept, in which groups differing in basic chromosome number are treated as distinct genera, the species discussed in the present paper would be placed in the genus *Tretorhiza* Adans.

Although a complete generic description of *Gentiana* is not included here, it does appear to be necessary to discuss certain features of the corolla because of their unusual nature and because of the diversity of terms which have been used in describing them. The corolla of *Gentiana* consists of five (occasionally four or six, rarely more) united petals, each of which terminates in a corolla lobe. Within the corolla tube, each of the primary divisions

[1] Contribution No. 22 from the Royal Botanical Gardens, Hamilton, Ontario, Canada.

SIDA 7(2): 174—217. 1977.

is separated from the next by a triangular segment of corolla tissue, which is invaginated in bud and to some extent at anthesis, and which is vascularized only distally by branches from the lateral veins of the two adjacent petals. These structures are called "appendages" in this paper, following such works as the *Flora Europaea* (Tutin, 1972); in some other publications on *Gentiana*, they have been termed "plicae" or "plaits."

The corollas of *Gentiana*, dextrorsely contorted in bud, emerge from the calyces long before anthesis. Until the corolla opens, part of each lobe is overlapped by part of the next lobe clockwise, except in a few species with greatly reduced lobes. The margin of the corolla lobe exposed in bud is termed the "outer margin" in this paper, and the other margin is termed the "inner margin." This use of "outer" and "inner" is to be distinguished from references to the exterior and interior (i.e., abaxial and adaxial) surfaces of the corolla.

Kusnezow's (1894) monograph of *Gentiana* "subgenus *Eugentiana*" and his (1895) treatment of *Gentiana* in Engler & Prantl's *Die natürlichen Pflanzenfamilien* provide the generally accepted basis for the division of *Gentiana* into sections, although some later authors have proposed refinements. Kusnezow's "subgenus *Engentiana*" is equivalent to *Gentiana* as the genus is circumscribed in this paper and in the recent publications cited above.

Only two sections of *Gentiana* are represented in Mexico and Central America, viz., sect. *Pneumonanthe* Gaudin and sect. *Chondrophyllae* Bunge. This paper deals with the taxonomy and distribution of sect. *Pneumonanthe*.

Key to the Sections of *Gentiana* in Mexico and Central America

1a. Small plants, usually less than 8 cm tall, with slender, fibrous roots; leaves less than 1 cm long; flowers less than 2 cm in length or diameter; free portions of corolla appendages nearly symmetrical, 2/3 to fully as long as lobes; gynophore slender, elongating in fruit so that the ovary is largely or completely exserted from the marcescent corolla. . . . . sect. *Chondrophyllae*.

1b. Plants usually well over 8 cm tall; tap root large and persistent, or replaced by several stout, fleshy secondary roots; larger leaves over 2 cm long; flowers over 2 cm long; free portions of corolla appendages more or less oblique, much exceeded by lobes (in Mexican and Central American species); gynophore variable, but not elongating sufficiently to exsert the entire ovary from the marcescent corolla. sect. *Pneumonanthe*.

GENTIANA [sect.] PNEUMONANTHE Gaudin, Fl. Helv. 2:269. 1828. Type species (Art. 22, ICBN): *Gentiana pneumonanthe* L.

Pneumonanthe Gled. (pro gen.), Syst. Pl. p. 238. 1764. Type species (only species definitely included): *Gentiana pneumonanthe* L., as *Pneumonanthe* [sp.].

Gentiana . . . *Pneumonanthe* Link (sine ord.), Enumeratio Pl. Hort. Reg. 1:258. 1821.

Gentiana subgenus *Pneumonanthe* Raf., Med. Fl. 1:208. 1828. Type species (Art. 22, ICBN): *Gentiana pneumonanthe* L.

Xolemia Raf. (pro gen.), Fl. Tellur. 3:22. "1836" [1837]. Lectotype species (hoc loc.): *Gentiana saponaria* L.

Xolemia subgenus *Cutlera* Raf., Fl. Tellur. 3:23. "1836" [1837]. Lectotype species (hoc loc.): *Gentiana catesbaei* Walt., as *Xolemia catesbei* [sic] (Walt.) Raf.

Gentiana sect. *Cyane* Griseb. in Hook., Fl. Bor.-Amer. 2:54. "1840" [1837]. Type species (Art. 7, ICBN; see Pringle, in press): *Gentiana pneumonanthe* L.

Perennials. Roots either several-many, thick, fleshy, and individually usually of short duration, or, in other species, consisting of a stout, persistent tap root and several smaller secondary roots. Rhizomes short and erect (geocorms). Stems 1-several, terete, generally over 5 cm long and in some species often over 1 m, ascending to erect, or in some species commonly decumbent at base, usually unbranched or with short, peduncle-like branches only. Rosettes of leaves absent except in seedlings. Leaf and calyx-lobe margins entire, minutely denticulate, or ciliolate, in most species neither cartilaginous nor scarious. Flowers erect (or somewhat declined in *G. caliculata* Lex.), 2.5-7.5 cm long. Calyx tubes either 15-nerved or 10-nerved through fusion of lateral sepal veins, cylindrical to vase-shaped, or in some species either occasionally or regularly cleft and spathelike. Intracalycular membrane generally well developed. Corollas ranging from completely closed to wide open at anthesis, open corollas closing at night and in cloudy weather but not thigmonastic. Corolla tubes cylindric to funnelform, vase-shaped, or urceolate. Corolla lobes shorter than tubes, deltoid to ovate-elliptic, or, in *G. andrewsii* Griseb., reduced to mucros. Free portions of corolla appendages usually well developed, basically bifid, usually oblique, with the sinus next to outer margin of each corolla lobe being deeper than the one next to inner margin, and the appendage segment next to the shallower sinus being narrower, but sometimes longer, than the other segment; in some species with the segment next to the inner corolla-lobe margin greatly reduced and deflexed, appearing as a projection from the lobe, or obsolete. Free portions of appendages in a few species symmetrical but well developed, in a few other species reduced to 2 small teeth or nearly obsolete. Summits of appendages (when well developed) ranging from subentire, erose, or minutely serrate (in species with one segment reduced) to shallowly to deeply laciniate, or shallowly fimbriate to deeply setose-fimbriate. Corollas of most species predominantly dark to light blue or violet-blue, with occasional forms having lilac, rose-violet, or white corollas; corollas of some species regularly violet, white, yellowish-white, or greenish-white; those of *G. caliculata* Lex. and *G. mirandae* Paray red. Darker stripes usually present on the interior surface of the tube, between primary veins of petals. Stamens equal, with straight filaments. Anthers connate (in all species with closed or nearly closed corollas, and in some species with open corollas) or free. Pollen grains oblate-spheroid to prolate, with sexine distinctly and often coarsely striate. Ovary compressed lance-ovoid, gradually

tapering into a short style, the style not sharply demarcated at anthesis and not spirally twisted (except tardily in *G. caliculata*). Stigmatic lobes linguliform or in a few species more slender, recurving. Gynophore relatively short and stout, usually 0.5-1.5 cm long and 1.5-2 mm thick at anthesis (longer and more slender in *G. mirandae*), elongating somewhat in fruit but not so as to elevate the entire ovary above the marcescent corolla. Carpels each with 1 dorsal and 6 ventral vascular bundles. Ovules distributed all over interior surface of ovary except in the immediate vicinity of sutures. Seeds with an obscurely to prominently reticulate testa, the testa in most species being expanded into a membranous wing partially or completely surrounding body of seed. $2n = 26$ in all taxa for which chromosome counts have been published. Sectional description compiled from Kusnezow (1895), Lindsey (1940), Toyokuni (1953), Nilsson (1967), standard references to published chromosome counts, and my own observations.

The foregoing description does not provide for *G. asclepiadea* L. because various lines of evidence suggest that this species may be misplaced in sect. *Pneumonanthe*. The generic name *Dasystephana* Adans., typified by *G. asclepiadea*, has therefore been omitted from the synonymy, along with the illegitimate modification *Dasistepha* Raf. *Gentiana newberryi* A. Gray and *G. tiogana* Heller have likewise been excluded from consideration, since their inclusion in this section also appears to be questionable.

The generic names *Ciminalis* Adans., *Diploma* Raf., *Ericoila* Borkh. (nom. illeg., altered to *Ericala* by some authors), *Hippion* F.W. Schmidt (nom. illeg.), and *Tretorhiza* Adans. emend. Löve & Löve are typified by species in other sections of *Gentiana*. Therefore, they have been excluded from the synonymy of sect. *Pneumonanthe*, although some authors have transferred species in sect. *Pneumonanthe* to these "genera."

Considerable variation exists in the orthography of the name of this section and in the authorship to which it has been attributed. Reasons for citing Gaudin (1828) as the author of the name *Gentiana* sect. *Pneumonanthe* have been given previously (Pringle, in press).

The formal subdivision of sect. *Pneumonanthe*, which would require consideration of variation patterns throughout its range, is not within the scope of this paper. The Mexican and Central American species of this section can, however, be informally divided into two groups. The first group, comprising *G. bicuspidata*, *G. ovatiloba*, and *G. hooperi*, is characterized by irregular, unpaired branching, if any, and by ebracteolate flowers. The other group, which includes *G. spathacea*, *G. laevigata*, and *G. caliculata*, differs in having isocladous branching, if any, with the flowers being borne in symmetrical, usually condensed cymes, and in the presence of paired bracts subtending each flower. *Gentiana mirandae*, because of the paired bracts subtending the flowers, can also be included in the latter group, although its branching is not always strictly isocladous.

In its entirety, sect. *Pneumonanthe* comprises about 50 species, native to North America from Guatemala north to Alaska and Labrador; to most of

Europe, except for the warmer, lowland regions; and to much of Asia, including the Caucasus, the Himalaya, central and southern Soviet Asia, central, southern, and eastern China, and Japan. Throughout the range of this section, its representatives are largely confined to humid or subhumid, warm-temperate to boreal regions. Those native to tropical latitudes, including the Mexican and Guatemalan species, are restricted to high elevations.

In the present paper, references to the physiographic provinces in which *Gentiana* species occur follow Raisz (1964). References to vegetational zones in Mexico follow Leopold (1950) and Flores Mata et al. (1971). Most Mexican species of sect. *Pneumonanthe* occur in the coniferous forest (bosque de coníferas) of Flores Mata et al. Its lowest subdivision, the pine-oak forest (bosque de pino-encino) of both Leopold and Flores Mata et al., is extensive in Mexico, occupying much of the higher terrain in the Sierra Madre Occidental, Sierra Madre Oriental, Neovolcanic Plateau, and Sierra Madre del Sur. It was further subdivided by Leopold, with the pine-oak woodland probably being the most important subdivision as a habitat of species in sect. *Pneumonanthe*, although they also occur in openings in the pine forest. *Gentiana* species are also present in the vegetational zones at higher altitudes on the Neovolcanic Plateau, including the transitional pine-alder-fir forest of Leopold (ca. 2200 m to 2300-2600 m), the fir forest (bosque de oyamel) (up to 2900-3200 m), and the relatively open *Pinus hartwegii* Lindl. forest (bosque de pino), which extends to treeline about 3600 m. Treeless alpine meadows (zacatonales of Flores Mata et al.) on the highest mountains are the habitat of one species in sect. *Pneumonanthe*.

In the Sierra Madre del Sur and the Chiapas-Guatemala Highlands and along the eastern rim of the Neovolcanic Plateau, the cloud forest of Leopold—termed deciduous forest (bosque de caducifolio) by Flores Mata et al., although it includes some pines—prevails above 1500 m and constitutes the principal habitat of the representatives of sect. *Pneumonanthe* in these ranges. In the highest mountains, *Pinus rudis* Endl. reaches higher elevations than other tree species, forming open woodlands in which *Gentiana* is also present.

The vegetation and major physiographic features of Guatemala, the only Central American country in which sect. *Pneumonanthe* is represented, have been mapped by Steyermark (1950). Two physiographic regions in Guatemala are mentioned in the present paper, namely, the Sierra de los Cuchumatanes, which is a part of Los Altos of Raisz (1964), and the Sierra Madre of Guatemala, which is continuous with the Sierra de Chiapas of southern Mexico. *Gentiana* species occur in the temperate-cold upland forest of Steyermark (equivalent, within the context of the present study, to Leopold's cloud forest), and in the alpine zones.

Populations of *G. bicuspidata*, *G. hooperi*, *G. mirandae*, *G. ovatiloba*, and *G. spathacea* have been studied in the field. Also, specimens have been examined from the following herbaria (abbreviations from Holmgren & Keu-

ken, 1974): A, ASU, BH, CAN, CAS, COLO, CU, DS, DUKE, ENCB, F, GH, HAM, ILL, MEXU, MICH, MIN, MO, MSC, MU, NCU, NY, POM, RSA, TAES, TENN, TEX, UC, US, VT, WTU, and WVA. Only a representative selection of specimens has been cited for each species, except for the newly described *G. hooperi* and the rarely collected *G. mirandae*, for which all known collections are listed. A complete list of specimens examined has been placed in the Depository of Unpublished Data, National Science Library, Ottawa, Canada, from which copies can be obtained, as well as in the library of the Royal Botanical Gardens, Hamilton, Ontario.

The chromosome counts reported in this paper are the first for any Mexican species of *Gentiana*. For *G. bicuspidata* and *G. spathacea*, the voucher specimens cited are those from which seed was obtained in the field. Chromosome counts were obtained from the seedlings. Root tips were pretreated in a saturated solution of α-bromonaphthalene for 2.5 hr at 18-20°C, fixed in Farmer's fluid, and stained with acetocarmine. Root tips of *G. ovatiloba* were obtained from plants collected in the field and were immediately fixed in Farmer's fluid. The illustrations of chromosomes are tracings from photomicrographs.

Species concepts in the present work take into account the remarkable extent to which interfertility has persisted among morphologically diverse species in sect. *Pneumonanthe*. The frequency of natural interspecific hybridization in this section is correlated more closely with the similarity of the geographic and ecological ranges of the parental species than with morphological similarities. Consequently, the mere existence of intermediates cannot be accepted as a practical basis for the amalgamation or reduction in rank of two taxa that would otherwise be treated as two species. Species have been accepted at this rank if the great majority of specimens seen could definitely be identified as belonging to one species or the other, with any intermediates evidently representing exceptional local populations rather than true intergradation. Experience with sect. *Pneumonanthe* in Canada and the United States has indicated that species meeting this criterion, even if the differences between them are not great, are nevertheless likely to be more sharply defined than any of the more inclusive taxonomic units one might attempt to assemble.

Key to the Mexican and Central American Species of Sect. *Pneumonanthe*

1a. Corollas red; stamens exserted.

2a. Calyx lobes arcuate-recurved; corolla lobes reflexed; corolla appendages bifid, ca. 1 mm long; gynophore much shorter than ovary at anthesis. . . . . 6. *G. caliculata*

2b. Calyx and corolla lobes erect or nearly so; corolla appendages obliquely triangular, ca. 2 mm long; gynophore about as long as ovary at anthesis. . . . . 7. *G. mirandae*.

1b. Corollas blue, violet, or nearly white; stamens included.

3a. Branching, if any, irregular, the branches usually only one at a node; flowers solitary at ends of stems or branches, or in raceme-like in-

florescences, not individually subtended by small bracts; corolla tubes vase-shaped or broadly campanulate.

4a. Corolla lobes violet-blue, contrasting with the white appendages; calyx lobes linear-subulate, 2-5 mm long, noticeably shorter than tube; corolla tube slender below, flaring only in upper half. . . . . 3. *G. hooperi.*

4b. Corolla lobes and appendages concolorous, blue, violet, or nearly white; calyx lobes linear to ovate-elliptic, about as long as tube or longer; corolla tube flaring from near base.

5a. Leaves linear; upper internodes longer than middle and lower ones, often over 2 cm long; calyx lobes linear; corolla lobes more or less orbicular, apiculate; flowers solitary, each terminating an unbranched stem or a distinct branch usually over 1 cm long. . . . . 1. *G. bicuspidata.*

5b. Leaves elliptic, closely spaced throughout; calyx lobes elliptic to ovate; corolla lobes ovate, rounded at apex when fully expanded; flowers solitary or in rather dense racemes of 2-8, the peduncle-like branches usually less than 1 cm long. . . 2. *G. ovatiloba.*

3b. Branching, if any, isocladous; flowers clustered in compact cymes or heads, individually subtended by small bracts; corolla tubes cylindric to narrowly urceolate-campanulate.

6a. Leaves broadly lanceolate to ovate, with 3-7 prominent veins, neither falcate nor strongly conduplicate; calyx usually largely hyaline, deeply cleft, with minute lobes; corolla lobes elliptic, apiculate. . . . . 4. *G. spathacea.*

6b. Leaves linear to narrowly oblong, usually with only the midvein prominent, upper leaves usually conspicuously falcate and conduplicate; calyx usually green and uncleft, with lobes 2-7 mm long; corolla lobes deltoid-ovate, usually obtuse or rounded at the apex. . . . . 5. *G. laevigata.*

1. GENTIANA BICUSPIDATA (G. Don) Briq., Candollea 4:324. 1931. Fig. 1.

Pneumonanthe bicuspidata G. Don, Gen. Hist. 4:194. "1838" [1837].

Based on *Gentiana assurgens* Sessé & Mociño, ined. Lectotype (hoc loc.): MEXICO: no further locality data, *Mociño & Sessé s.n.*, no date, OXF, photos in HAM!; probable duplicates, *Sessé et al. 1368* (number assigned by curator at MA), no date, F!, MA, and (unnumbered) GH!

Gentiana assurgens Sessé & Mociño ex G. Don, Gen. Hist. 4:194. "1838" [1837], pro syn.

Gentiana adsurgens Cerv. ex Griseb. in Hook., Fl. Bor.-Amer. 2:57. "1845" [1837] (in ablative, "*adsurgente*"), nomen nudum; Cerv. ex Griseb., Gen. Sp. Gentianearum p. 286. "1839" [1838], with description. Type collection: *Sesse et al. 1368*, cited under *Pneumonanthe bicuspidata* G. Don, above.

Gentiana adsurgens [var.] β *uniflora* Kusn., Trudy S.-Peterburgsk. Obshch. Estestvoisp., Otd. Bot. 24(2):61. 1894. Syntypes: MEXICO: [Distrito

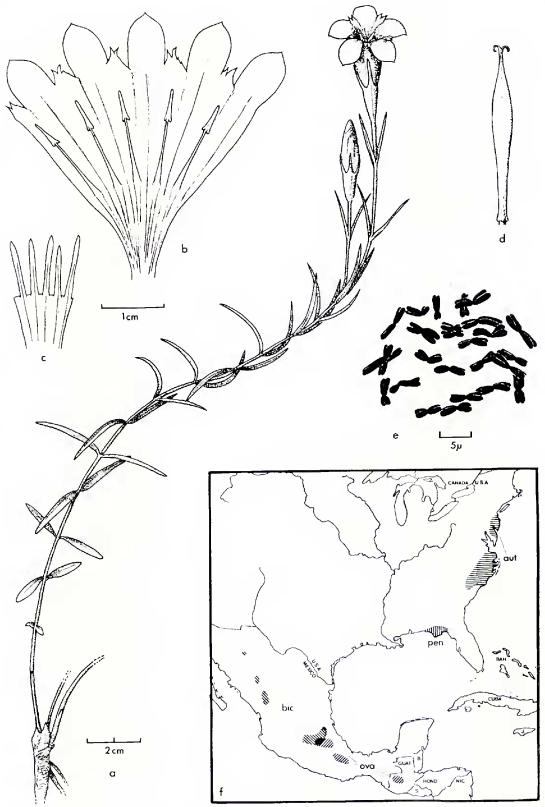

Fig. 1. *Gentiana bicuspidata.* a, flowering stem; b, interior surface of corolla, and c, exterior surface of calyx, slit longitudinally and pressed; d, pistil; e, somatic chromosomes; f, ranges of *G. autumnalis* (aut), *G. bicuspidata* (bic), *G. ovatiloba* (ova), and *G. pennelliana* (pen).

Federal]: Desierto Viejo, Valle de México, *Bourgeau 1123*, 17 Oct 1866, B (probably not extant), LE (uncited duplicates in GH!, MICH!, US!, and probably elsewhere; and MEXICO: no further locality data, *Ehrenberg s.n.*, B (probably not extant), LE (uncited duplicate in MEXU!).

Gentiana angusta M.E. Jones, Contr. W. Bot. 12:52. 1908. Probable type: MEXICO: Chihuahua: Mound Valley, Sierra Madre Mts., alt. 7000 ft, *Jones s.n.*, 18 Sep 1903, DS!

Tap root usually well developed and persistent, 0.8-1.5 cm in diameter at the summit and 0.5-1.5 dm long, often forked, or occasionally accompanied or replaced by 2-several subequal secondary roots. Stems usually 1-6, occasionally up to 12 or more, decumbent to suberect, 1-4 dm long, papillose-puberulent in lines below the leaf bases, otherwise glabrous, usually simple, occasionally with 1-4 branches. Leaves bright green, linear or lowest ones narrowly elliptic, longest near middle of stem, only moderately reduced above and below, except near soil level, upper internodes often appreciably longer than lower and middle ones. Upper leaves acute at apex, lower leaves obtuse, all tapering at base. Leaves mostly 1.5-5.5 cm long, upper ones usually 20-30 times as long as broad, occasionally broader, median ones 8-15 times as long as broad, lowest ones highly variable in proportions. Leaf margins minutely and shallowly denticulate, usually more or less revolute. Flowers solitary at ends of stems or branches, without involucres, the uppermost leaves usually well separated from base of flower. Calyx tube uncleft, 7-17 mm long, glabrous. Calyx lobes erect, linear to narrowly oblong, 5-10(-20) mm long, acute. Corolla 3-5.5 cm long, the tube funnelform, increasing gradually in diameter from the base upward. Corolla lobes spreading, elliptic or sometimes obovate, (5.5-)7-12 mm long, apices abruptly acuminate to rounded-apiculate, margins sparingly erose-serrate to subentire, sinus adjacent to outer edge of each lobe slightly deeper than the other. Free portions of corolla appendages 2-5 mm long, subequally bifid, primary divisions often further cleft, ultimate segments acuminate to attenuate. Lower ½-¾ of corolla tube pale, exterior surface of the petals proper suffused with bronze-purple, interior surface with purplish-blue stripes between the central and lateral veins of petals and with small purplish-blue spots elsewhere. Upper ¼-½ of corolla tube, lobes, and free portions of appendages pale to deep blue throughout, with the purplish suffusions on exterior surface extending to outer margins of lobes and a green suffusion extending to all but inner margin, and prominent yellowish-green spots on interior surface of the lower half of lobes and adjacent portions of tube. Stamen filaments becoming free a little below middle of corolla tube, free portions 7.5-10.5 mm long. Anthers ca. 5 mm long, not cohering. Fruits slightly to more than half exserted at anthesis. Seeds ca. 2 mm long, 0.9 mm wide, completely winged. $2n = 26$ (voucher specimen: MEXICO: Hidalgo: 4.8 km N of Agua Blanca Iturbide, *J.S. Pringle 1303a*, 28 Jan 1972, HAM).

Most populations of *G. bicuspidata* are in the Neovolcanic Plateau and in

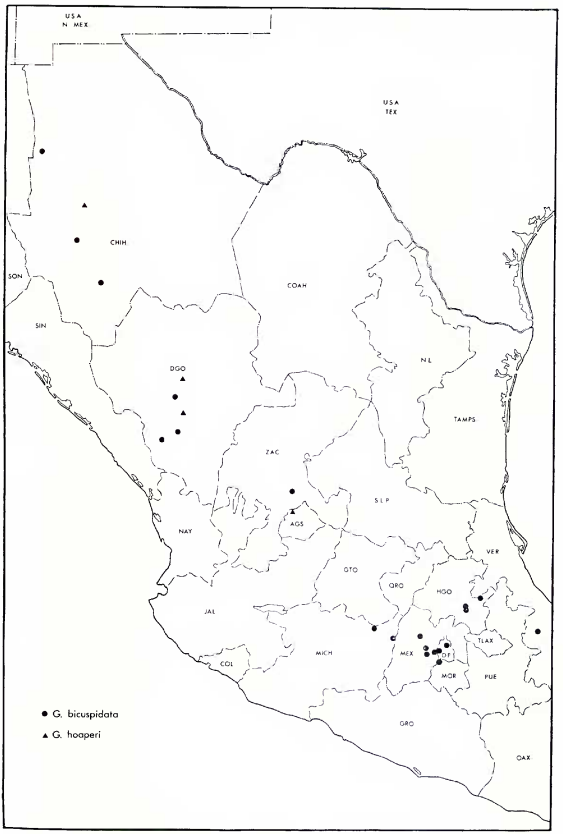

Fig. 2. Documented distribution of *Gentiana bicuspidata* and *G. hooperi*.

the adjacent southernmost portion of the Sierra Madre Oriental (Sierra de Pachuca), from Hidalgo west to northeastern Michoacán, with disjunct populations occurring in the Sierra Madre Occidental in Durango and southern Chihuahua (Fig. 2). Its usual habitat is a consistently moist meadow, often near a stream or pond, most frequently in the pine-alder-fir zone, sometimes in the fir forest zone, or, in its easternmost populations, in the northern outliers of the cloud forest. Specimens have been collected in flower from September through March.

Representative specimens examined:

MEXICO: Chihuahua: near Guacochic, *Goldman 179* (GH, US). Distrito Federal: Cerro del Tepalcate, cerca del Puerto de Las Cruces, *Rzedowski 21727* (DS, ENCB, F, MEXU, MICH, TEX, WIS). Durango: 8 mi NW of Estación Coyotes, *Breedlove 18778* (MICH). Hidalgo: Sierra de Pachuca, *C.G. Pringle 15007* (ASU, CAS, CM, COLO, F, GH, MICH, MSC, TEX, UC, US, VT). México: Valley of Toluca, *C.G. Pringle 4309* (CAS, F, GH, MEXU, MICH, MO, MSC, MU, NY, RSA, UC, US, VT). Michoacán: 6-7 mi N of San Pedro Aguaro, *McVaugh & Wilbur 9991* (MICH). Morelos: head of Lake Zempoala, *Correll 14282* (DUKE). Veracruz: Palo Bendito, Huayacocotla, *Hernández M. & Yolanda de Hdez. 974* (GH). Zacatecas: *Coulter 951* (K; photos in HAM seen).

The names *Pneumonanthe bicuspidata* G. Don and *Gentiana adsurgens* Cerv. ex Griseb. appear to have been based on the same collection, although on different specimens. This collection was made during the period 1788-1804 at some unspecified Mexican locality by the botanical expedition headed by Martín Sessé L., which included J.M. Mociño and Vincente Cervantes among its members (Standley, 1920). Sessé & Mociño designated this collection *Gentiana assurgens* in herb., but this name did not appear in their published works.

Don (1837) based the name *Pneumonanthe bicuspidata* on *Gentiana assurgens* Sessé & Mociño. His acquaintance with unpublished names proposed by Sessé & Mociño was based on duplicates of their collections in the herbarium of A.B. Lambert (as indicated in Don, 1837, passim). Sessé & Mociño collections from Lambert's herbarium are now in BM, G, and OXF (Miller, 1970). Of these three herbaria, only OXF contains a specimen of their *Gentiana assurgens*. Since this appears to be the only specimen of this collection likely to have been seen by Don, it has been selected as the lectotype of the name *Pneumonanthe bicuspidata* G. Don.

According to Miller (1970), Lambert received his Sessé & Mociño specimens from J.A. Pavón, who had selected duplicate material from that left at MA by Mociño. The annotation "Guayaquilensis" on the specimen of "*Gentiana assurgens*" at OXF may have been added by someone who confused *Gentiana assurgens* Sessé & Mociño, ined., with *Selatium assurgens* D. Don ex G. Don, which was based on a specimen in the Lambert herbarium collected by Ruiz & Pavón or Tafella at Guayaquil, and which was equated with *Gentiana guayaquilensis* Griseb. in *Index Kewensis*. Although

obviously erroneous, this annotation does help to link the OXF specimen to Lambert's herbarium and thus to Don.

Additional specimens that may be duplicates of the same collection by the Sessé expedition are at MA and F; those at F were examined during the present study. These bear Sessé & Mociño's label "*Gentiana assurgens* N[obis]" and the number *1368*, which was assigned by a curator at MA. Another collection, or possibly additional duplicates of the same collection, bear the label "*Gentiana adsurgens*" and the number *682*. In addition to the replicates of *Sessé et al. 1368* and *682* at MA and F, there is an unnumbered specimen in the type collection at GH labeled "*Gentiana assurgens* sp. n. Mexico" and, in another hand, "Cervantes" following the binomial, and "Fielding his writing?" This specimen is probably a duplicate of *Sessé et al. 1368* or *682*. All of the specimens in F, GH, and OXF cited above clearly represent the species treated here as *G. bicuspidata*.

Grisebach (1838), in publishing the name *G. adsurgens*, attributed the origin of this name to Cervantes. Cervantes never published this name, but presumably used it in herb. or in ms. The relationship between names proposed or published by Cervantes and those proposed or published by Sessé & Mociño has been discussed by McVaugh (1945), who concluded that "we are probably justified in supposing that the Sessé and Mociño plants [in MA and F] are to be regarded as the types of Cervantes' species." The name *G. adsurgens* Cerv. ex Griseb., therefore, seems to be best typified by the Sessé expedition collection numbered *1368*. The specimen seen by Grisebach may have been in B, where Grisebach worked on his *Genera et Species Gentianearum*, in which case it would not be extant.

Whether the specific epithet *bicuspidata* has priority over *adsurgens* has been the subject of some discussion (Briquet, 1931; Williams, 1968). Accord to Stafleu (1967), the first part of Vol. 4 of Don's *General History of the Dichlamydeous Plants* (which probably included *Pneumonanthe bicuspidata*) was published in 1837, and the entire volume had been published by 8 Apr 1838 or earlier. Grisebach's *Genera et Species Gentianearum*, in which this species was first described under the name *Gentiana adsurgens*, was published in early Oct 1838. Therefore, I accept *bicuspidata* as being the correct specific epithet for this taxon.

Gentiana bicuspidata is morphologically similar to *G. autumnalis* L., a species native to the Atlantic Coastal Plain from South Carolina to New Jersey. The most evident differences between these two species are as follows: The free portions of the corolla appendages of *G. bicuspidata* are triangular and are bifid near the summit, while those of *G. autumnalis* are proportionately lower and much divided; the margins of the corolla lobes of *G. bicuspidata* are entire or only slightly erose, while those of *G. autumnalis* are prominently erose-serrate; the calyx lobes of *G. bicuspidata* are abruptly acute, while those of *G. autumnalis* are acuminate; the tap root of *G. bicuspidata* is usually persistent and well developed, while that of *G. autumnalis* is soon replaced by several lesser roots; and the seed wing of

G. bicuspidata is much more prominent than that of *G. autumnalis*. *G. bicuspidata* averages lower in stature and probably higher in number of stems per plant than *G. autumnalis*, but there is considerable overlapping in the ranges of variation in both of these traits. The somatic chromosome number of 26, reported here for *G. bicuspidata*, has also been reported for *G. autumnalis* (as *G. porphyrio* J.F. Gmel.) by Rork (1949).

Gentiana bicuspidata and *G. autumnalis*, along with *G. ovatiloba* of Mexico and Guatemala and *G. pennelliana* Fern. of Florida, appear to be closely related, all having the characteristics of the "first group" of species recognized above, as well as having widely open corollas with large lobes and deeply cleft appendages, free anthers, more or less decumbent stems, and, with the exception of *G. ovatiloba*, linear leaves. The distribution of this group of closely related species (Fig. 1f) corresponds to a pattern recognized by many biogeographers, in which identical or closely related taxa occur on the Atlantic Coastal Plain of the United States and disjunctly in the highlands of central and southern Mexico. Species or groups exhibiting the distribution pattern may have different phytogeographic histories. In the case of the *G. autumnalis-G. bicuspidata* complex, however, it appears probable that its colonization of Mexico and Guatemala occurred subsequent to its establishment in northern North America, and that the Mexican and Guatemalan species were derived from an ancestral complex centered in more northern latitudes, rather than vice versa. This interpretation is indicated by the fact that sect. *Pneumonanthe* is distributed predominantly in North Temperate, rather than tropical, latitudes, with its southernmost populations being restricted to relatively cool, montane habitats, and both of the groups distinguished above are more widely distributed and more diverse in northern North America than in Mexico and Guatemala. The extent of the distribution of this complex both north and south of the disjunction in its range and its differentiation into two species in each segment of its range indicate that this complex has had a relatively long history in both regions, rather than having recently colonized one of these regions through long-distance dispersal.

The scattered populations of *G. bicuspidata* in the Sierra Madre Occidental may be remnants of a more extensive and more nearly continuous distribution in the past, when climatic conditions permitted greater development of mesic vegetation. The assumption that the northwestern outliers of *G. bicuspidata* are relictual could account for patterns of variation in this species. Such traits as relatively short corolla lobes in some specimens from Chihuahua may be due to past introgression of genetic material from the *G. affinis* complex when both species-groups were more widely distributed in western North America; reciprocal introgression may account for the occurrence of long-branched individuals of *G. affinis* (= *G. interrupta* Greene) near the Mexican-United States border.

Plants of this species bearing only one flower per stem were segregated by Kusnzow (1894) as *G. adsurgens* [var.] β *uniflora*. Herbarium and field

studies of *G. bicuspidata* indicate that such variation commonly occurs among plants in a single population and even among the stems on a single plant, and is without taxonomic significance.

Gentiana angusta was described by Jones (1908) from plants found 18 Sep 1903 "in meadows along with other gentians, Mound Valley, Sierra Madre Mts., Chihuahua . . . at 7000 feet alt." In the paper in which he described *G. angusta*, Jones stated that the type specimens of all new names published therein were in his personal herbarium. No such specimen is at POM, which later acquired Jones's herbarium, but a collection reasonably compatible with Jones's description of *G. angusta*, and bearing identical data, is at DS, one of the many herbaria to which Jones sent specimens during his lifetime. This collection comprises three plants mounted on one sheet, all of which are entirely characteristic of *G. bicuspidata*, except that the corolla lobes are relatively short for this species. This collection is labeled "*Gentiana linifolia*," with no author's name. It seems probable that this is the type collection for the name *G. angusta*. *Gentiana linifolia* may have been Jones's first choice for a name for these plants and may later have been replaced in his paper but not corrected on the label when he found that this name was preoccupied. These specimens do indicate clearly that a collection of *G. bicuspidata* was made by Jones at Mound Valley on 18 Sep 1903 and was considered by him to represent a taxon to which no name then in use should be applied (the names *G. linifolia* Salisb. and *G. linifolia* Willd. ex Schult., based on European plants, having long since passed into obscurity). For these reasons, and because no other Jones specimens of *Gentiana* from Mound Valley appear to exist, *G. angusta* M.E. Jones is treated here as being a taxonomic synonym of *G. bicuspidata* (G. Don) Briq.

2. GENTIANA OVATILOBA Kusn., Trudy Imp. S.-Peterburgsk. Bot. Sada (Acta Horti Petrop.) 13:60. 1893. Type: MEXICO: [Distrito Federal]: Desierto Viejo, Valle de México, *Bourgeau 1123-bis*, 17 Oct 1856, holotype LE, isotype (not cited by Kusnezow) GH!

Gentiana caespitosa Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(1):370. 1844, non *G. cespitosa* Willd. ex Schult. in Roem. & Schult., Syst. Veg. 4:185. 1819, nec *G. caespitosa* R. Graham, Edinburgh New Philos. J. 10:367. 1830. Type: MEXICO: Veracruz: Pic d'Orizaba, 10000 [Paris ft], *Galeotti 1483*, "184-" (date incomplete, probably actually 1838), P, photos in F!, MO!, NY!

Gentiana guatemalensis Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:75. 1944. Type: GUATEMALA: Huehuetenango: alpine meadow, region of Chémal, Sierra de los Cuchumatanes, alt. about 3300 m, *Standley 81113*, 28 Dec 1940, holotype F!, isotype GH!

Gentiana lewisiae Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:76. 1944. Type: GUATEMALA: Totonicapán: damp meadow, Pacajá, region of Desconsuelo, mountains above Totonicapán, alt. 3100-3200 m, *Standley 84556*, 23 Jan 1940, F!

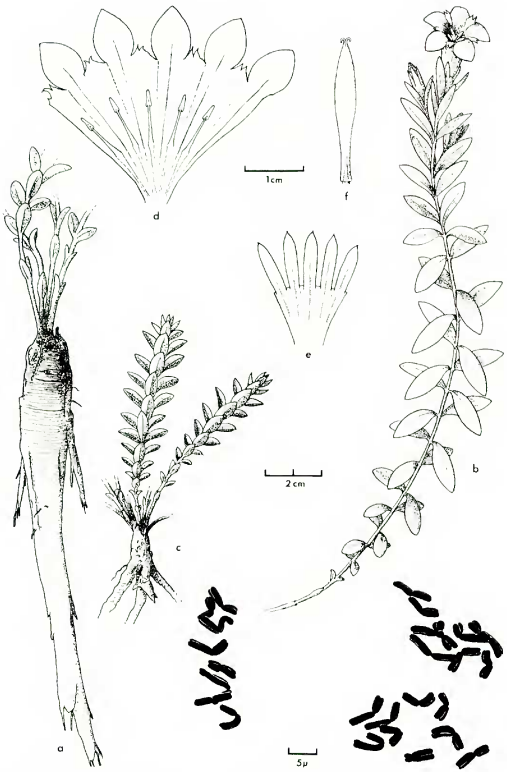

Fig. 3. *Gentiana ovatiloba*. a, root of plant from deep soil; b, flowering stem; c, portion of plant from dry, shallow soil; d, interior surface of corolla, and e, exterior surface of calyx, slit longitudinally and pressed; f, pistil; g, somatic chromosomes.

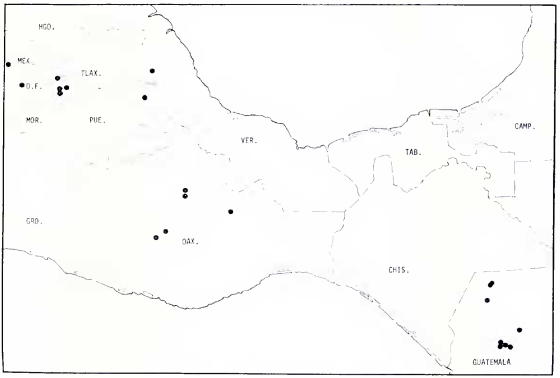

Fig. 4. Documented distribution of *Gentiana ovatiloba*.

Tap root usually persistent, 1-1.8 cm in diameter at summit and 0.7-1.5 dm long, often forked distally and producing branch roots; older plants often bearing many stout secondary roots from branches and divisions of the geocorm, these divisions sometimes becoming essentially independent. Stems cespitose, usually 2-12, occasionally more, decumbent to erect, 1-6 dm long, glabrous except for a few minute projections in lines below leaf bases, simple or with 1-7 short branches near summit. Leaves somewhat succulent, bright green, elliptic, largest near middle of stem, only the lowest much reduced, evenly and closely spaced, obtuse to rounded at apex, rounded at base. Leaf margins smooth, flat or somewhat revolute. Largest leaves 1-3 cm long, 2.5-3.5 times as long as broad. Flowers solitary or in racemose or corymbose clusters of 1-8 through the production of short branches near summit of main stem. Flowers usually closely subtended by uppermost pair of leaves, but without differentiated bracts. Calyx tube uncleft, 6.5-10 mm long, glabrous. Calyx lobes erect, oblong to narrowly elliptic-ovate, 5-12 mm long, obtuse, sometimes apiculate. Corolla 2.5-4.5 cm long, the tube funnelform. Corolla lobes spreading, ovate-triangular or broadly ovate to elliptic-rhombic, 3.5-8.5 mm long, sparingly erose-serrate to nearly entire, the apices obtuse to acute, the sinuses subequal. Free portions of the appendages 2-4 mm long, basically bifid with the segments variously toothed or cleft, the

ultimate divisions acute to attenuate. Lower ¾ of corolla tube pale, increasingly suffused with blue upward, with bronze-purple suffusions on exterior surfaces of petals proper, and purplish stripes (varying in distinctness) on interior surfaces between midvein and lateral veins. Upper part of corolla tube, lobes, and free portions of appendages blue, exterior surface of lobes suffused with green except near inner margin, and with bronze-purple near outer margin. Blue pigment sometimes very pale, or replaced by violet. Interior corolla surfaces unspotted or (in northern populations) with a few yellowish-green spots near base of lobes. Stamen filaments becoming free about ¼ the height of corolla tube, free portions 4.5-6 mm long. Anthers ca. 3.5 mm long, not cohering. Fruit slightly exserted from marcescent corolla at maturity. Seeds similar to those of *G. bicuspidata*. $2n = 26$ (voucher specimen: MEXICO: México: Cañada de Alcalican, SW side of Ixtaccíhuatl, *J.S. Pringle & T. Duncan 1509*, 22 Jun 1974, HAM).

Gentiana ovatiloba grows in the highest mountains in the Neovolcanic belt from western Veracruz west to the Distrito Federal, and in the Sierra Madre del Sur in Oaxaca. Disjunct populations are present in the mountains of western Guatemala (Fig. 4). Reports of "*G. adsurgens*" in Chiapas, e.g. by Standley & Williams (1969), which one might expect to have been based on *G. ovatiloba*, actually appear to have been based on specimens of *G. laevigata*. *Gentiana ovatiloba* is usually found in the alpine grasslands just above treeline, with occasional populations extending to open, exposed sites in the *Pinus hartwegii* or *P. rudis* zones. Most plants of *G. ovatiloba* are found along streams and in seasonally moist depressions, associated more with rushes and mesophytic forbs than with the dominant bunchgrasses. Occasional plants, however, occur in shallow, dry soils near rock outcrops. The flowering season extends from August to March, and sporadically through the summer in some populations.

Representative specimens examined:

GUATEMALA: Huehuetenango: 7 mi N of Santa Eulalia, *Breedlove 8597* (DS, F, US). Sololá: 10-12 km NW of Los Encuentros, *Williams et al. 27307* (F, NY). Totonicapán: about 12 km SW of Totonicapán, *Williams et al. 25462* (F, NY, US). MEXICO: México: Cañada de Alcalican, Ixtaccíhuatl, *Rzedowski 21569* (DS, ENCB, MICH, WIS). Oaxaca: Zempoaltepetl, *Camp 2666* (A, MICH, NY, RSA, UC). Puebla: ládera NE de Ixtaccíhuatl, *Ern 309* (ENCB). Veracruz: Cofre de Perote, NW side of mountain, *Beaman 2189* (GH, MSC).

Collections of *G. ovatiloba* from Guatemala have consistently been recognized as being specifically distinct from *G. bicuspidata*. Standley & Steyermark (1944) and Standley & Williams (1969) considered *G. guatemalensis* and *G. lewisiae*, as they designated these plants, to be endemic to Guatemala, evidently having accepted the Mexican representatives of this complex as being "*G. adsurgens*." In recent years, specimens from Oaxaca have, with increasing frequency, been equated taxonomically with the Guatemalan material, usually as *G. guatemalensis*. To date, however, specimens

virtually indistinguishable from the Guatemalan plants have generally been included in *G. bicuspidata* (or "*G. adsurgens*") if they were collected north of Oaxaca.

The most conspicuous differences between *G. ovatiloba* and *G. bicuspidata* are the following. The leaves and calyx lobes of *G. ovatiloba* are proportionately much wider than those of *G. bicuspidata*. The leaves of *G. ovatiloba* are more closely spaced than those of *G. bicuspidata*, especially toward the summit of the stem, where the leaves of *G. bicuspidata* are often widely separated. *Gentiana bicuspidata* sometimes produces flowering branches several cm long, with two or more pairs of leaves, whereas the branches of *G. ovatiloba* are almost always short and peduncle-like. The corolla lobes of *G. ovatiloba* are ovate to ovate-triangular and are blunt; those of *G. bicuspidata* are elliptic to suborbicular, widest near or above the middle, and are generally apiculate. The interior surface of the corolla of *G. bicuspidata* is conspicuously spotted with yellowish-green, especially near the base of the lobes; such spots are usually absent from the corollas of *G. ovatiloba*, although not invariably so in the northernmost part of its range. The free portions of the corolla appendages of *G. bicuspidata* tend to be proportionately longer than those of *G. ovatiloba*. Both the stamen filaments and the anthers of *G. bicuspidata* are longer than those of *G. ovatiloba*, with the anthers of the former thus being nearer the throat of the corolla.

Despite this rather extensive list of differences, *G. ovatiloba* and *G. bicuspidata* appear to be very closely related. Most plants of this complex can be readily and unequivocally assigned to one or the other of these species, but occasional specimens deviate from the typical form of one species in having one or more traits, usually vegetative, like those of the other species. For example, *Lyonnet 458* (GH, NY, US), from the Desierto Viejo, Distrito Federal, where both *G. bicuspidata* and *G. ovatiloba* have been collected, is typical of the former species in general habit and in corolla morphology but has exceptionally broad, blunt leaves and calyx lobes. A duplicate of this collection in F, however, falls within the usual range of variation in *G. bicuspidata*. A joint, but independently numbered, collection by Pringle & Smith from the Sierra de Clavellinas, southwest of the city of Oaxaca (*C.G. Pringle 4985*, GH, MICH, US, VT; *Smith 752*, MO, NY), and *Nelson 1400* (GH, US), from the same general area, consist of plants that are typical of *G. ovatiloba* in habit, leaf spacing, and floral morphology but have narrower leaves (mostly 2-4 mm wide) than those ordinarily found in this species.

Most of the alpine zones constituting the habitat of *G. ovatiloba* are at elevations that resulted from Pliocene and Pleistocene uplift and volcanic activity, with the exception of those in the somewhat older Sierra de los Cuchumatanes in the southern part of its range. This association with relatively recently formed habitats suggests that *G. ovatiloba* is probably the latest product of evolution in the *G. bicuspidata* complex, representing an adaptation to alpine conditions.

Standley & Steyermark (1944), as noted above, treated the Guatemalan representatives of *G. ovatiloba* as two species, *G. guatemalensis* and *G. lewisiae*, which were originally contrasted as follows: *G. guatemalensis*—flowers 1-3 per stem; calyx tube ca. 8 mm long; calyx lobes ca. 10 mm long; corolla ca. 2.5 cm long; segments of the free portions of the corolla appendages acute to acuminate, sparsely serrate. *G. lewisiae*—flowers solitary; calyx tube 5-6 mm long; calyx lobes 4-7 mm long; corolla ca. 2 cm long; segments of the free portions of the appendages rounded, entire. In 1969, however, both *G. guatemalensis* and *G. lewisiae* were described by Standley & Williams as having 1-few flowers per stem. These authors then noted that *G. guatemalensis* and *G. lewisiae* "are perhaps too much alike and the distinctions tend to disappear with additional collections."

As mapped by Steyermark (1950), the alpine zones, which are the habitat of *G. ovatiloba*, are restricted to two areas in Guatemala: the Sierra de los Cuchumatanes, the source of the more northern records for Guatemala mapped in Fig. 4; and the Sierra Madre, the source of the records for southern Guatemala. Thus isolated from each other as well as from the Mexican populations, these Guatemalan populations do appear to have differentiated to the extent that plants from the Sierra Madre tend to be smaller, in stature and in the size of their leaves and flowers, than plants from the Sierra de los Cuchumatanes or from Mexican populations. However, the study of additional Guatemalan material which has become available since the description of *G. guatemalensis* and *G. lewisiae*, the inclusion of specimens from Mexico as well as from Guatemala in the present study, and field observations of sizeable populations occupying diverse microhabitats indicate that *G. guatemalensis* and *G. lewisiae* cannot justifiably be maintained as separate species. Quantitative variation appears to be essentially continuous within this species, with no evident discontinuity separating the Sierra Madre plants from those of other regions. No qualitative differences were discerned between the type specimens of *G. lewisiae* and *G. guatemalensis*, or between specimens from the Sierra Madre and those from the Sierra de los Cuchumatanes or from Mexico. The divisions of the corolla appendages appear to be as acute in the type collection of *G. lewisiae*, and in other specimens from the Sierra Madre which have been identified as *G. lewisiae*, as in the type collection of *G. guatemalensis* or in other specimens from Guatemala or Mexico.

Limited local variation also appears to have developed among the Mexican populations of *G. ovatiloba*. As I observed on Ixtaccíhuatl, for example, stems of large and small plants alike bore only one flower per stem, whereas in the Sierra Juárez, Oaxaca, flowers were almost invariably borne in racemes of two or more. Within the Ixtaccíhuatl population, variation not evidently correlated with environmental factors was noted in corolla color and lobe length. Microenvironmental factors also appear to contribute significantly to variability of *G. ovatiloba*; plants in relatively dry, exposed sites differ conspicuously in stem height and in spacing and condu-

plicateness of the leaves from those growing among dense vegetation in wet depressions (Figs. 3b and 3c).

3. GENTIANA **hcoperi** Pringle, species nova. Fig. 5.

Herba perennis, glabra. Caules 1-6, ascendentes, 0.3-2 dm longi. Folia griseo-viridia, aliquanto succulenta, obtusa, maxima 2-4.5 cm longa in parte caulis inferiore. Flores vulgo solitarii, interdum racemosi 2-4, exinvolucrati. Tubus calycis infissus, 8-16 mm longus. Lobi calycis linear-subulati, acuminati, 2-5 mm longi. Corolla infundibuliformis, 3.5-5.5 cm longa. Lobi corollae elliptico-obovati, patentes, 6-10 mm longi, 4.5-9 mm lati, integres, obtusi, violaceo-lazulini, albomarginati, e viridi-purpureo extra. Partes librae plicarum 2-4 mm longae, 3-5 mm latae, bifidae segmentis laciniatis, medium tubi corollae; partes librae 5-7 mm longae.

Type: MEXICO: Aguascalientes: Municipio San José de la Gracia, high plateau in the Sierra Fría ca. 8 km SW of La Congoja, ca. 22° 10′ N, 102° 33′ W, 7 Feb 1972, *J.S. Pringle 1320* (holotype HAM, isotypes CAN, HAM, K, MEXU, MICH, NY, S, TENN). Topo-paratype, from the same locality, expressed as " 'Sierra Fría' 15 mi W of Presa Calles": *Hooper* 10 Mar 1953 (MICH). Additional paratypes: MEXICO: Chihuahua: vicinity of Miñaca, *Rose 11645* (US). Durango: Sierra de San Francisco, *Foshag* Feb 1941 (MEXU); Sierra de Carcaría, near Rio Verde, *Foshag* 28 Feb 1941 (ENCB, US).

Several subequal roots 1.5-8 mm in diameter usually present. Stems 1-6, decumbent to ascending, 0.3-2 dm long, glabrous, simple or with 1-4 short branches. Leaves gray-green, often suffused with purple, rather succulent, somewhat conduplicate, especially upper ones, linear or lower ones narrowly elliptic to oblanceolate, obtuse at extreme apex, tapering at base, upper leaves strongly ascending, median and lower leaves moderately ascending or spreading. Leaf margins very narrowly cartilaginous, minutely denticulate proximally, entire distally, the cartilaginous margin usually abruptly widened in distal 1-3 mm. Leaves largest on lower half of stem, upper leaves gradually reduced to 1/3-2/3 the length of the largest leaves, only those near and below the soil line scalelike. Largest leaves 2-4.5 cm long, (4-)8-30 times as long as wide. Flowers solitary at end of main stem and branches, occasionally appearing racemose if several reduced branches are present, exinvolucrate or subtended only by uppermost pair of leaves. Calyx tube uncleft, 8-16 mm long, glabrous. Calyx lobes erect, linear-subulate, 2-5 mm long, acuminate. Corolla 3.5-5.5 cm long, tube funnelform, with lower half slender, widening very gradually upward, upper half more abruptly flaring. Corolla lobes spreading, elliptic-obovate, 6-10 mm long, 4.5-7(-9) mm wide, entire, obtuse, sinuses about equal on both sides. Free portions of appendages 2-4 mm long, 3-5 mm wide, bifid, divisions further irregularly toothed or cleft, ultimate segments acute to attenuate. Corolla tube greenish-white below, increasingly suffused upward with violet-blue and externally with green, in the petals proper. Corolla lobes violet-blue (often similar in color to corollas of typical *Vinca minor* L., sometimes

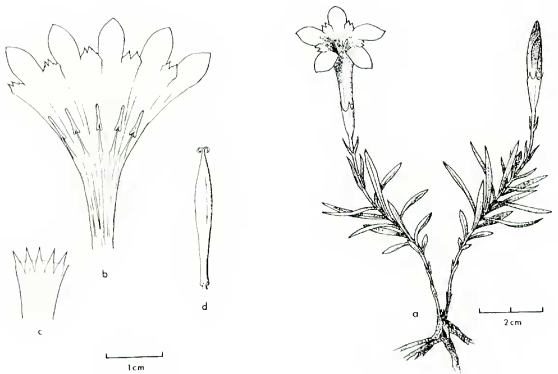

Fig. 5. *Gentiana hooperi*. a, flowering plant; b, interior surface of corolla, and c, exterior surface of calyx, slit longitudinally and pressed; d, pistil.

paler or bluer, occasionally nearly white), narrowly white-margined, the exterior surface suffused with green except near inner margin, and with purple near outer margin. Dark blue-violet, usually interrupted, streaks present on inner surface of the upper ¼-½ of corolla tube between midrib and lateral veins of each petal, extending into the lobes as rows of dots; additional spots or short streaks occasionally present at juncture of petals proper and appendages. Midribs narrowly outlined with green on both surfaces. Appendages white throughout, or fused portions with a faint to prominent blue patch on each side near summit. Stamen filaments becoming free at or slightly below middle of corolla tube, free portions 5-7 mm long. Anthers free at anthesis. Fruit and seeds not seen.

Gentiana hooperi is named for Emmet T. Hooper, Curator of Mammals, University of Michigan Museum of Zoology, whose collection of this species was the first I saw, and whose directions enabled me to visit the type locality.

To date, *G. hooperi* has been collected only at four widely separated localities, all in the lower, eastern ranges of the Sierra Madre Occidental (Fig. 2). At the type locality in the Sierra Fria in northwestern Aguascalientes, some plants of *G. hooperi* were found in swampy sites (dry at flower-

ing time) among relatively dense stands of *Juncus* species and other graminoids. Other plants grew on higher ground where only a sparse herbaceous layer was present, among widely scattered small trees of *Juniperus deppeana* Steud., some of the gentians being in seasonally moist depressions, others in very dry, exposed sites. *Gentiana hooperi* was just coming into bloom when the type collection was made in early February; the other collections, for which dates are given above, also comprise plants in flower.

The slender corolla tube of *G. hooperi*, which flares widely only near the summit, and the linear, succulent, gray-green leaves give this species an aspect superficially similar to that of some species in sect. *Frigidae* Kusn. The leaf margins also resemble those of species in sect. *Frigidae*. The habit of growth of *G. hooperi*, however, clearly indicates that its affinity is with sect. *Pneumonanthe*, since species in sect. *Frigidae* have slender, creeping rhizomes from which either overwintering or permanent rosettes arise. The well-developed, bifid free portions of the corolla appendages of *G. hooperi* are also more characteristic of sect. *Pneumonanthe* than of sect. *Frigidae*.

The closest relatives of *G. hooperi* are probably *G. bicuspidata* and *G. ovatiloba*. It is, however, well differentiated from these species and may have had a relatively long history of isolation. Although additional populations of *G. hooperi* may remain to be discovered, its distribution is obviously sporadic and disjunct and is probably best regarded as comprising the remnants of a more nearly continuous distribution in the past.

Gentiana hooperi is generally of lower stature than *G. bicuspidata*, even when plants growing in apparently similar habitats are compared. The leaves of these species differ markedly in color and texture. The acuteness of the upper leaves of *G. bicuspidata* also contributes to the difference in aspect between it and *G. hooperi*. The calyx lobes of *G. hooperi* are shorter and, in contrast to the leaves, more sharply pointed than those of *G. bicuspidata*.

The corolla of *G. hooperi* is significantly different is shape from that of *G. bicuspidata*, the corolla tube of *G. hooperi* being prolonged and slender, as noted above, in contrast to the proportionately broader corolla tube of *G. bicuspidata*. The corolla lobes of *G. bicuspidata* are usually apiculate, whereas those of *G. hooperi* are obtuse (although the inrolling of the margins, before the corolla has fully expanded, may temporarily create the appearance of apiculate lobes on newly opened corollas). The illustrations of these species show the marked difference in the levels at which the stamens become free from the corolla tubes.

Two aspects of corolla pigmentation present especially obvious differences between *G. hooperi* and *G. bicuspidata*. The basic color of the corollas of *G. hooperi* is a slightly grayed periwinkle-blue, with an appreciable violet content, while that of the corollas of *G. bicuspidata* is a true blue, varying in intensity but with very little violet content. The predominantly white free portions of the appendages of *G. hooperi* are conspicuous and contrast with the blue lobes. In *G. bicuspidata*, the lobes and appendages are similar in

color. Other differences between *G. hooperi* and *G. bicuspidata* can be noted from the descriptions and illustrations of these species.

4. GENTIANA SPATHACEA H.B.K., Nov. Gen. Sp. 3:173 (quarto text). "1818" [1819].

Type: MEXICO: [Veracruz]: in declivitate orientali montium Mexicanorum, prope urbem Xalapae, alt. 700 hex., *Humboldt s.n.*, no date, P, photos in F!, MO!, US! Fig. 6.

Gentiana plicata Willd. ex Schult. in Roem. & Schult., Syst. Veg. 6:185. 1820. Type: duplicate of type collection of *Gentiana spathacea*, cited above, B-herb. Willd., photos in HAM!

Coilantha sessaei D. Don ex G. Don, Gen. Hist. 4:185. 1837. Type: MEXICO: no further locality data published, *Sessé et al.* collection formerly in herb. A.B. Lambert, not located, probably not extant. (Ex char.)

Coilantha mocinni D. Don Ex G. Don, Gen. Hist. 4:185. 1837. Type: MEXICO: no further locality data published, *Sessé et al.* collection formerly in herb. A.B. Lambert, not located, probably not extant. (Ex char.)

Ericala spathacea (H.B.K.) G. Don, Gen. Hist. 4:191. 1837.

Gentiana ovalis Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(1):369. 1844. Type: MEXICO: [Veracruz]: Xalapa, 6000 [Paris ft], *Galeotti 1486*, no date, G, photos in F!, GH!, MICH!, NY!, US!

Gentiana sessaei (G. Don) Griseb. in DC., Prodr. 9:112. 1845.

Gentiana spathacea [var.] *β Benthami* Griseb. in DC., Prodr. 9:113. 1845. Type: MEXICO: [Hidalgo]: Velasco, prope Real del Monte, *Hartweg 349*, 1839, holotype K, photos in F!, MICH!, isotype NY!

Gentiana coerulea Sessé & Mociño, Naturaleza (Mexico City), ser. 2, 1(App.):44. 1888, etiam *G. caerulea* [sic] Sessé & Mociño ex G. Don, Gen. Hist. 4: 185. "1838" [1837], pro syn., et *G. coerulea* Sessé & Mociño ex. Griseb. in DC., Prodr. 9:112. 1845, pro syn., non *G. coerulea* Ruiz & Pavón ex Griseb., Gen. Sp. Gentianearum p. 235. "1839" [1838], pro syn. Type collection: MEXICO: no further locality data, *Sessé et al. 897* (no. assigned by a later curator at MA), no date, MA, F!

Gentiana spathacea [var.] *φ integra* Kusn., Trudy S.-Peterburgsk. Obshch. Estestvoisp., Otd. Bot. 24(2):53. 1894. No type indicated.

Pneumonanthe spathacea (H.B.K.) Greene, Leafl. Bot. Observ. Crit. 1:71. 1903.

Dasystephana spathacea (H.B.K.) Arthur, Torreya 19:49. 1919.

Tap root persistent, usually 1-2 cm in diameter at summit and 1.5-2 dm long, generally forked and bearing branch roots distally, often accompanied by several-many thick secondary roots arising from the elongating, sometimes much branched and divided geocorm. Stems 1-20(-50 or more), ascending to erect, 1-10 dm tall, minutely papillose-puberulent or glabrous. Leaves bright green, lanceolate to broadly ovate, prominently 3-nerved (the larger ones also having 1 or 2 pairs of less prominent nerves), rounded at base, acute at apex, with margins entire and minutely revolute. Larger leaves 2.5-8 cm long, 2-5(-6) times as long as wide. Leaves largest a short

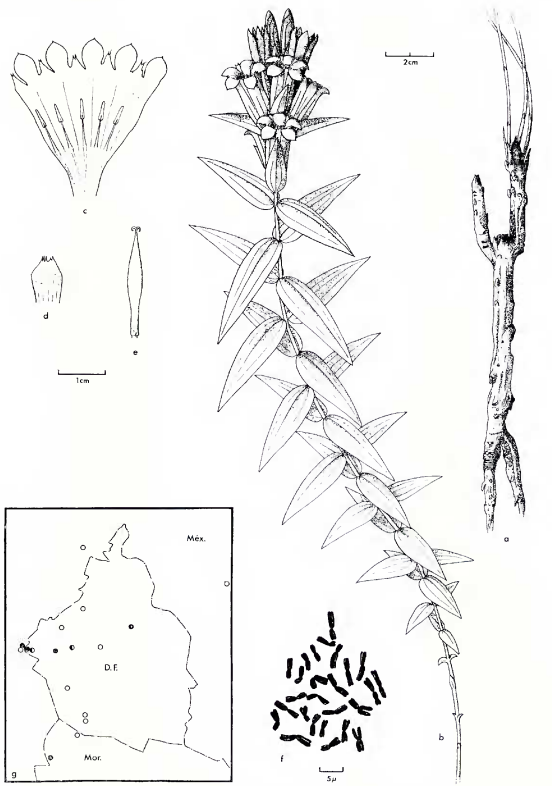

Fig. 6. *Gentiana spathacea*. a, underground portions; b, flowering stem; c, interior surface of corolla, and d, exterior surface of calyx, slit longitudinally and pressed; e, pistil; f, somatic chromosomes; g, documented distribution of *G. spathacea* (open circles), *G. bicuspidata* (closed circles), and mixed populations including hybrids (half-closed circles) in the Distrito Federal and vicinity.

distance below summit of stem, slightly reduced above, gradually reduced to small scales near base of stem. Flowers solitary or in small sessile or short-pedunculate groups in upper 1-8 (rarely more) axils and in terminal clusters of 3-30, those in clusters subtended by pairs of reduced leaves or linear bracts (see discussion below). Calyx tubes typically cleft to base on one side, hence spathelike, 5-10 mm long, herbaceous below, hyaline above, glabrous. Calyx lobes usually subulate, less than 1 mm long, closely spaced at summit of the tube opposite the cleft. Occasional plants with calyces larger, herbaceous throughout, less deeply or not at all cleft, with oblong-oblanceolate lobes up to 6 mm long and more evenly spaced. Corollas 2.5-4(-5) cm long, tubes urceolate-campanulate. Corolla lobes spreading, broadly ovate-elliptic to orbicular, 4-8(-10) mm long, 2.5-6.5 mm wide, entire, apiculate, sinuses on each side almost equally deep. Free portions of appendages erect, 3-6 mm long, 2.5-4 mm wide, tapering into 2 subequal, closely spaced, attenuate teeth, sometimes with lesser teeth or irregularities along the margin. Lower 2/5 of corolla tube whitish, remainder of corolla blue, becoming deeper in color upward, especially in the petals proper, the deep blue of lobes extending downward on interior surface of the tube in stripes between the midrib and lateral veins. Petals below the lobes, and the outer margin of each lobe, very dark and suffused with purple on exterior surface. Appendages lighter, but blue throughout. Stamen filaments becoming free at ca. 3/8 the height of corolla tube, free portions ca. 6 mm long. Anthers loosely coherent or free at anthesis, ca. 3 mm long. Fruits only slightly exserted from corolla at maturity. Seeds ca. 2 mm long, 0.7 mm wide, winged, wing very narrow on one side, $2n = 26$ (voucher specimen: Hidalgo: 2.6 km N of Mexico Hwy. 105 on road to Mineral del Chico, *J.S. Pringle 1305a*, 28 Jan 1972, HAM).

The range of *G. spathacea* largely coincides with the boundaries of the Neovolcanic Plateau, extending from Veracruz west to Jalisco, although it reaches the southernmost portions of the Sierra Madre Oriental in Hidalgo and southern San Luis Potosí and has been collected at one locality in the northwestern part of the Sierra Madre del Sur in Guerrero (Fig. 7). Most populations of *G. spathacea* are in the upper reaches of the pine-oak forest and in the pine-alder-fir zone; a few extend to the fir forest zone. Within these zones, the usual habitat of *G. spathacea* consists of partially shaded, generally well-drained slopes, often in a small opening or near the edge of the woods. Specimens have been collected in flower from August through April. Plants in the drier microhabitats usually bloom in autumn or early winter and may be found with ripe fruits and desiccated stems in late winter, while plants in moister sites are then in bloom.

Representative specimens examined:

MEXICO: Distrito Federal: Sierra de Ajusco, *C.G. Pringle 6221* (CAS, CM, F, GH, MEXU, MICH, MO, MSC, NY, TEX, UC, US, VT). Guanajuato: 2 mi S of Santa Rosa, *Harker & Mellowes 145* (ENCB, WIS). Hidalgo: Sierra de Pachuca, *C.G. Pringle 15006* (ASU, CAS, COLO, GH, MICH, MSC, TEX,

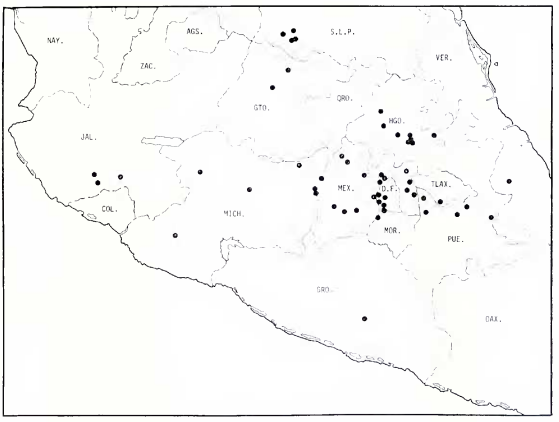

Fig. 7. Documented distribution of *Gentiana spathacea*.

UC, US, VT). Jalisco: Nevado de Colima, *McVaugh & Hoover 11615* (MEXU, MICH, US). México: Meson Viejo, *Hinton et al. 8973* (ENCB, F, GH, MICH, MO, NY, US). Michoacán: Zitácuaro - Copándiro, *Hinton et al. 13551* (MICH, NY, US). Morelos: Toro, *Matuda 21923* (MEXU). Puebla: near La Venta, *Sharp 441853* (GH, HAM, MEXU, MO, NCU, NY, TENN). San Luis Potosí: 5 km al N de Soledad de Zaragoza, *Rzedowski 7095* (ENCB, MEXU, TEX). Tlaxcala: am Fuss der Ruines Cacaxtla, *Seler & Seler 3556* (GH).

Gentiana spathacea appears to be most closely related to the *G. affinis* complex of western North America north of Mexico, although not exhibiting so close a relationship as that of *G. bicuspidata* to *G. autumnalis*. This group of species is also more widely distributed, and includes more taxa, in northern North America than in Mexico. At times during the Tertiary, northern, mesophytic species-groups were evidently more widely distributed in the Southern Rocky Mountains and the Sierra Madre Occidental; it seems likely, therefore, that the range of the *G. affinis-G. spathacea* group was more nearly continuous in the past, and variation within this group may formerly have been clinal. The present degree of differentiation of *G. spathacea* from related species, however, along with its extensive distribution and variability on the Neovolcanic Plateau and in adjacent regions, indi-

cates that this species has probably had a relatively long history in Mexico.

Gentiana rusbyi Greene ex A. Gray, from the Mogollón Mountains of New Mexico, was described (Gray, 1886) as being intermediate between *G. affinis* (as *G. bigelowii* A. Gray, a taxonomically insignificant variant) and *G. spathacea*. Examination of the type collection, *Rusby 263* (MICH, MO, NY), however, indicates that plants so designated are entirely typical of *G. affinis* in habit, foliage, and corolla morphology, differing only in having reduced calyx lobes. According to Hitchcock (1959), such plants occur sporadically throughout much of the range of *G. affinis* and do not warrant taxonomic recognition. It appears, therefore, that *G. rusbyi* should be included within *G. affinis* and need not be interpreted as connecting *G. affinis* with *G. spathacea*.

Variants of *G. spathacea* have been recognized taxonomically by several authors. It was first treated as more than one species by Don (1837), who divided it into three species in two genera. *Coilantha sessaei* was based on a Sessé & Mociño collection in the herbarium of A.B. Lambert, which had been designated *G. coerulea* by its collectors. The specimen seen by Don in Lambert's herbarium could not be located in BM, G, or OXF, the three herbaria known to have received Sessé expedition specimens from the Lambert herbarium. Examination of a duplicate of this collection in F, however, has confirmed that *G. coerulea* Sessé & Mociño, and hence *C. sessaei* G. Don, are synonymous with *G. spathacea* H.B.K.

Don's (1837) description of *Ericala spathacea* is simply a paraphrase of the description of *G. spathacea* by Humboldt et al. (1819), and contains no indication that Don had examined any specimens thus identified. It is not clear from Don's descriptions what he considered to be the most significant differences between *C. sessaei* and *E. spathacea* or why he placed them in different genera. The only point in which they were actually contrasted was that *C. sessaei* was said to have axillary flowers, whereas those of *E. spathacea* were described as being in terminal clusters. When Grisebach (1845) transferred *C. sessaei* to *Gentiana*, he distinguished it from *G. spathacea* chiefly by its lacking paired bracts beneath the flowers, according to Don's description of this taxon.

Don (1837) also described *Coilantha mocinni*, which was said to differ from *C. sessaei* in that it did have paired bracts beneath each flower. His description of *C. mocinni* as having 5-nerved, ovate-lanceolate leaves and a spathaceous calyx, and his statement that it, too, had been identified as *G. coerulea* Sessé & Mociño in Lambert's herbarium, indicate that it was also based on a specimen of *G. spathacea*, perhaps another specimen from the collection on which the name *C. sessaei* had been based. No specimen appropriate for the typification of the name *C. mocinni* could be found in BM, G, or OXF. Grisebach's (1845) treatment of this name as a synonym of *G. caliculata* Lex. was based only on Don's description of *C. mocinni* and was evidently due to Grisebach's admitted unfamiliarity with *G. caliculata*, of which he had then seen no specimens. Certainly the elements of

the description of *C. mocinni* noted above are inapplicable to *G. caliculata*.

To discuss the status of these segregates, it is necessary to consider the nature of the inflorescence of *G. spathacea*, which is basically a dichasial cyme. Within *G. spathacea*, there is a trend toward condensation of the inflorescence. Plants at one end of this trend have the entire inflorescence relatively open, so that at least the lower flowers may appear to be pedicellate and to be subtended only by "leaves," with no small bracts being present. In other plants, the pedicels, cyme branches, and upper internodes are very short or obsolete, and the leaves and bracts in the inflorescence are much reduced. In the most extreme expression of this trend, the inflorescence is more or less capitate, with the inner (theoretically upper) bracts, or some of them, minute or obsolete. Within a single population of *G. spathacea*, a wide range of variation in condensation of the inflorescence may be encountered. Small plants in the driest, most exposed microhabitats generally have small, terminal, capitate inflorescences, whereas plants in moister, more shaded sites are likely to have more longated inflorescences, with flower clusters or short flowering branches arising from several of the upper axils of the main stems. Otherwise, there is little obvious correlation between microhabitat and inflorescence form. Obviously, minor variation in such features as the length of cyme branches and pedicels, or the development of bracts, does not constitute a sound basis for taxonomic division of *G. spathacea*.

Martens & Galeotti (1844) segregated a solitary-flowered individual or individuals of *G. spathacea* with relatively broad leaves as *G. ovalis*. The solitary flower can almost certainly be attributed to the age of the plant or to adverse growing conditions. Leaf shape is variable within populations of *G. spathacea* and is evidently related to environmental factors. Plants in dry, sunny situations have relatively narrow leaves, which have a tendency to be ascending and somewhat conduplicate. Leaves of plants in moister, shadier sites, especially those leaves below the inflorescence, are proportionately wider, wide-spreading, and flat. The leaves of the type specimen of *G. ovalis* do not significantly exceed the range of variation in leaf shape commonly found in populations of *G. spathacea*.

An unnamed variant of *G. spathacea* was described by Bentham (1840) as having larger calyx teeth and frequently entire corolla appendages. This variant was given formal taxonomic status as *G. spathacea* var. *benthamii* ("*β Benthami*") by Grisebach (1845). Later, Kusnezow (1894) described var. *integra* as having an uncleft calyx with unequal, subulate teeth. (The calyx tube of var. *benthamii* was not described by Bentham or Grisebach but was evidently assumed by Kusnezow to have been cleft.)

Variability in calyx form exists throughout the range of *G. spathacea*. The type specimen of var. *benthamii* was collected in the vicinity of Real del Monte, Hidalgo, an area from which many specimens of *G. spathacea* have been obtained, most of them having the typical spathaceous calyces with minute lobes. Specimens approaching both extremes of variation, with

calyces ranging from hyaline and deeply cleft, with minute lobes, to herbaceous and uncleft, with lobes up to 6.5 mm long, may sometimes be found within a single collection, e.g., *Hinton 524* (US), from Temascaltepec, México, *Hinton et al. 13540* (F, GH, MICH, MO, NY, US) from the vicinity of Zitácuaro, Michoacán, or *Hinton et al. 15749* (DS, F, MEXU, NY, POM, UC, US), from Barroloso, Michoacán. There appears to be a trend toward less frequent and less extreme cleavage of the calyx tube and reduction of the calyx lobes in the western part of the range of *G. spathacea*, but plants from as far west as the vicinity of Autlán, Jalisco, exhibit considerable variation in these traits, even among the plants from a single population (*McVaugh et al. 10285* and *21320*, MICH). Except that large calyx lobes are generally associated with shallowly cleft or uncleft calyx tubes, the traits by which var. *benthamii* and var. *integra* were distinguished do not appear to be correlated with other morphological features. Neither the corolla lobes nor the free portions of the appendages of the holotype and isotype specimens of var. *benthamii* appear to differ appreciably from those of typical *G. spathacea*. Because of the sporadic occurrence of plants with relatively large calyx lobes and/or uncleft calyx tubes, formal taxonomic recognition of these variants seems to be unwarranted.

Plants collected in the vicinity of Pátzcuaro, Michoacán (*C.G. Pringle 3982*, MEXU, MSC, MU, NY, POM, UC, US, VT) are exceptional in that the stems had continued to elongate after the development of the lower axillary flower buds, so that, at the time of collection, clusters of flowers or buds, opening in acropetal sequence, were present in as many as 14 successive axils. *Moran 10075* (DS), from El Carmen, Hidalgo, has unusually large corollas for this species, ca. 5 cm long, with acuminate lobes ca. 10 mm long.

Gentiana spathacea is also variable in other, less conspicuous aspects. Plants in some populations have minutely papillose-puberulent stems, while plants in other populations have glabrous stems. (Most *Gentiana* species studied by me are consistent in having either puberulent or glabrous stems, but some, e.g., *G. saponaria* L., are similarly variable in this respect.) Within a single population of *G. spathacea*, one may encounter variation in whether the anthers are coherent or free; this variation may be correlated to some degree with the age of the flowers. Inrolling of the margins of the lobes of wilted or marcescent corollas may affect the superficial aspect of specimens prepared from such material.

The name *G. plicata* Willd. ex Schult. was not applied to a proposed segregate of this species but instead to the same collection that typifies the name *G. spathacea*, Schultes and Kunth having been working simultaneously on different sets of Humboldt's collections. In the present study, examination of photographs of the type specimen of *G. plicata* has confirmed that Humboldt et al. (1823) were correct in treating this name as a synonym of their own *G. spathacea*.

5. GENTIANA LAEVIGATA Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(1):370. 1844. Type: MEXICO: Oaxaca: Cordillera, Sierra, 5-7000 [Paris ft], *Galeotti 1481*, Nov-Apr 1840, G, photos in F!, MICH!, NY! (duplicates may be elsewhere). Fig. 8.

Tap root, if present, 2.5-5 mm thick, usually accompanied or replaced by several well-developed secondary roots. Stems 1-6, at least the basal portions decumbent, the distal portions varying from flexuous to erect, 1.5-5(-9) dm long, minutely but copiously papillose-puberulent below, sparsely papillose-puberulent to smooth above. Stems and leaves usually much suffused with reddish-purple. Lower leaves, or nearly all the leaves on short stems (exclusive of reduced leaves near soil line), lanceolate to oblong, nearly flat and widely spreading to moderately conduplicate and arcuate, with 1 or 3 prominent veins, 1.5-5 cm long, 3.5-6.5 times as long as wide, obtuse to subacute at apex, abruptly tapering at base. Lower internodes 0.8-3 cm long. Upper leaves similar in shape but increasingly conduplicate and arcuate, 1.5-3 cm long. Upper internodes of well-developed stems 4-9 cm long. Involucral leaves subtending terminal flower cluster in 1 or 2 pairs, lanceolate to ovate, 2-3.5 cm long, (3-)8-14 mm wide, acute at apex, abruptly tapering to strongly rounded at base, strongly conduplicate, arcuate, enveloping the lower part of flower cluster. Leaf margins entire, revolute. Flowers solitary or in clusters of 2-6, confined to the terminal cluster or also borne on short (up to 2.5 cm), peduncle-like branches from uppermost 1-4 nodes. Individual flowers subtended by linear bracts usually 10-15 mm long, occasionally larger and foliaceous. Calyx tubes typically uncleft, 7-12 mm long, glabrous, the portions enveloped by the involucral leaves often somewhat hyaline. Calyx lobes erect or nearly so, typically linear-subulate to narrowly oblong, 2.5-8 mm long, 0.2-2 mm wide, acute. Calyces of occasional plants deeply cleft, with greatly reduced lobes. Corollas (2.5-)3-4 cm long, tube urceolate-cylindric, gradually expanding upward. Corolla lobes spreading, ovate-triangular, 3.5-7 mm long, as wide or slightly wider than long, minutely erose-serrate to nearly entire, obtuse or occasionally apiculate, sinuses subequal. Free portions of appendages asymmetrical, consisting of 2 nearly equal, attenuate teeth each 1.5-2 mm long and 0.5-1.2 mm wide, and an erose shoulder 1.8-3 mm wide extending to outer edge of the next lobe clockwise. Lower half of corolla tube whitish, tube increasingly suffused with blue upward, uppermost part of the tube, the lobes, and the free portions of the appendages deep blue throughout. Exterior surface of corolla with purplish suffusions as in *G. spathacea*. Blue pigment extending downward on interior surface of tube as prominent stripes between central and lateral petal veins. Stamen filaments becoming free at ca. 2/5 the height of corolla tube, free portions 10-12 mm long. Anthers loosely connate or free. Summit of ovary about even with tips of marcescent corolla in mature fruit. Seeds ca. 1.8 mm long and 0.8 mm long and 0.8 mm wide, winged, wing very narrow along one side.

Gentiana laevigata is evidently endemic to the Sierra Madre del Sur in Oaxaca, and to Los Altos, a subdivision of the Chiapas-Guatemala Highlands

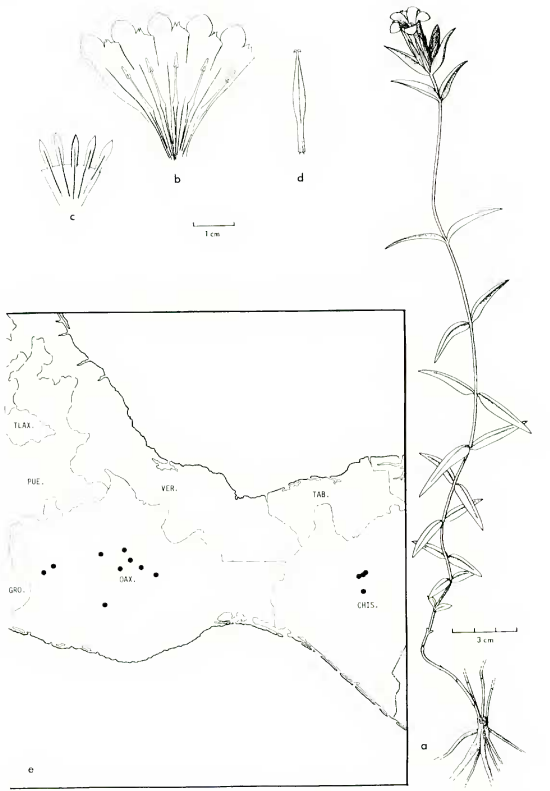

Fig. 8. *Gentiana laevigata*. a, flowering stem; b, interior surface of corolla, and c, exterior of calyx, slit longitudinally and pressed; d, pistil; e, documented distribution.

in Chiapas (Fig. 8e). Its usual habitat consists of grassy slopes in the pine-oak zone and in the lower portions of the cloud forest. Flowering occurs from August through February.

Representative specimens examined:

MEXICO: Chiapas: between Las Casas and Ejido "El Triunfo," *Sharp 45994* (MEXU, NY, TENN); barrio of Tuk, paraje of Matsab, Municipio of Tenejapa, *Breedlove 12443* (DS, F, MICH); 9 mi SE of San Cristóbal Las Casas, *Breedlove & Raven 13421* (DS, F); near Zinacantán center, *Laughlin 2705* (DS, US). Oaxaca: Santa Inés del Monte, *Conzatti 1348* (GH, MEXU); near Tlaxiaco, *Camp 2264* (NY); halfway from Guelatao to Llano de las Flores, *Vilas 332A, 332B* (WIS).

Gentiana laevigata is represented by relatively few collections. It occurs in small, widely scattered populations that exhibit some local differentiation in morphological traits. The majority of specimens, however, including all those cited above, are very similar to one another and to the type specimen. These specimens, therefore, were regarded as being most representative of *G. laevigata* in the preparation of the description of this species.

Gentiana laevigata appears to be a derivative of *G. spathacea* or its immediate ancestor, which became established in southern Mexico after orogenic processes had created suitable habitats. Its range in the mountains of Oaxaca and Chiapas is isolated from that of *G. spathacea* by the intervening lower and drier Mixtec Upland.

Gentiana laevigata and *G. spathacea* differ most conspicuously in their general habit and foliage. The stems of *G. spathacea* are relatively stout and are ascending to erect, or decumbent only near the base. Mature plants growing in favorable sites usually produce many stems. The stems of *G. laevigata*, in contrast, are slender and often flexuous, *Laughlin 2705* (DS, US) having been described as a "vine," and seldom number more than three or four per plant. *Gentiana spathacea* is usually densely leafy, whereas the upper leaves of *G. laevigata* are widely spaced. Also, the leaves of *G. laevigata* are proportionately wider than those of *G. spathacea*. The upper leaves of *G. laevigata* are generally somewhat arcuate and strongly conduplicate, in contrast to those of *G. spathacea*, which are not arcuate and seldom strongly conduplicate except in sun forms.

The corolla lobes of *G. laevigata* are broadly deltoid-ovate, and the apices are usually obtuse or rounded. Thus they contrast with the elliptic, strongly apiculate corolla lobes of *G. spathacea*. Also, the free portions of the corolla appendages of *G. laevigata* are definitely asymmetrical, consisting of two teeth and an erose "shoulder," whereas those of *G. spathacea* are nearly symmetrically divided into two teeth only. *Gentiana laevigata* differs further from *G. spathacea* in its proportionately longer stamens.

Both *G. laevigata* and *G. spathacea* are variable in calyx form. Typical plants of *G. laevigata* differ from those of *G. spathacea* in having uncleft calyces with well-developed, subequal lobes. Occasional plants of *G. laevigata*, e.g., *C.G. Pringle 5647* (GH, MICH, VT), collected near Las Sedas,

Oaxaca, differ from the typical form of this species in having cleft calyx tubes. *Ghiesbreght 718* (MO), from the vicinity of San Cristóbal Las Casas, Chiapas, and *MacDougall 2616* (NY), collected between La Cumbre and Ixtlán de Juárez, Oaxaca, include flowers with cleft and uncleft calyces on the same sheet.

Specimens collected between Tamazulapa and Ayutla, Oaxaca (*Camp 2725*, NY) exhibit unusual branching and have proportionately wider leaves than are commonly encountered in *G. laevigata*, although the flowers are entirely characteristic of this species. On one of the plants in this collection, there are three slender branches 1-1.5 dm long, plus several leafy tufts, borne near the base of the main stem, in addition to branches up to 3 cm long from the upper five axils. The branches terminate in clusters of relatively small flowers. Another plant on the same sheet has branches ca. 1.5 cm long from the upper three axils only.

6. GENTIANA CALICULATA Lex. in La Llave & Lex., Nov. Veg. Descr. p. 18. 1824. Type: MEXICO: [Michoacán]: prope Santa María, oppidum indianum juxta Vallisoletum, no further collection data, not located, probably not extant. (Ex char.) Neotype (hoc loc.): MEXICO: [México]: in sylvis prope Temascaltepec, *Ehrenberg s.n.*, no date (probably Apr 1831), MEXU! Fig. 9.

Gentiana salpinx Griseb., Linnaea 22:44. 1849. Type: MEXICO: [México]: in sylvis prope Temascaltepec, *Ehrenberg 450*, Apr 1831, holotype formerly in B, probably not extant; neotype of *Gentiana caliculata*, cited above, is probably an unnumbered duplicate of the same collection; other duplicates may be elsewhere.

Root system comprising several subequal, fleshy roots (according to Lexarza, in La Llave & Lexarza, 1824). Stems 1-few, ascending to erect, 0.4-1.6 m tall, minutely papillose-puberulent. Lower leaves (except for scalelike leaves near soil line) ovate to elliptic, flat, 3-5-nerved, 3-9 cm long, 1-4 cm wide (length/width ratio variable), acute at apex, rounded at base, often marcescent at flowering time. Lower internodes 2-3 cm long. Median leaves smaller and more distantly spaced, elliptic-oblong, flat to moderately conduplicate, 1-3-nerved, acute at apex, truncate at base. Upper leaves linear, strongly conduplicate and arcuate, 1-nerved, 1.5-5 cm long, 1-6 cm wide, acute to acuminate at apex, tapering at base. Upper internodes usually 5-15 cm long. Leaf margins entire, revolute. Cymes terminal and on short (or occasionally elongate, up to 1.5 dm long) branches from the upper 2-8 nodes, the branches often arching toward tip, the two branches arising from opposite sides of the same node usually being curved in the same direction, the inflorescence, or at least its lower part, thus being more or less secund. Flowers solitary or in small, dense clusters (often in pairs), individually short-pedicellate or sessile. Cymes, their divisions, and individual flowers subtended by linear strongly arcuate and conduplicate, acuminate, minutely ciliolate bracts, those subtending cymes usually 2-3 cm long, 2-4 mm wide, those subtending individual flowers or pairs of flowers 1-2 cm long, 1-2 mm

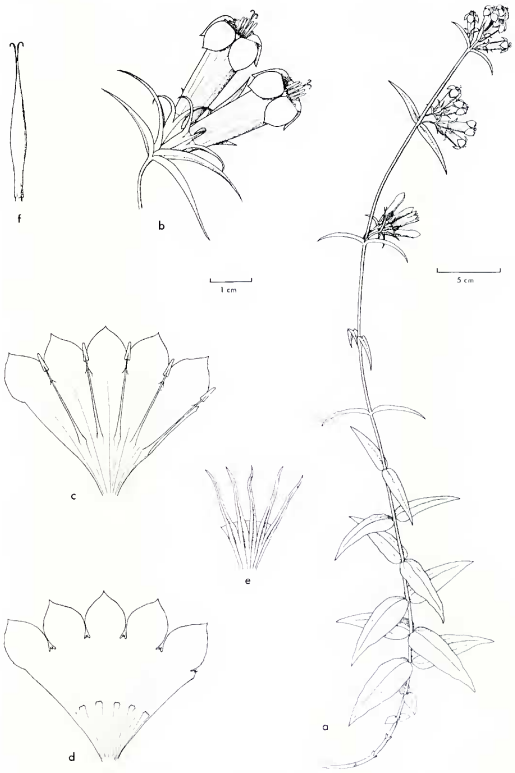

Fig. 9. *Gentiana caliculata.* a, flowering stem; b, a pair of flowers with subtending bracts; c-d, interior surfaces of corollas, with stamens present (c) and stamens removed (d), and e, exterior surface of calyx, slit longitudinally and pressed; f, pistil.

wide. Calyx tubes uncleft, 6-16 mm long, minutely but copiously puberulent. Calyx lobes linear, strongly arcuate-recurved, 6-20 mm long, puberulent and ciliolate. Corolla tubes 2.5-4 cm long, flaring just above summit of calyx tube, otherwise nearly cylindrical. Corolla lobes reflexed, 6.5-15 mm long, oblong-ovate to nearly orbicular, apiculate, margins often erose-serrate, especially near base, sinuses subequal. Free portions of appendages consisting of 2 approximately equal, acuminate to attenuate teeth each 1.5-2 mm long and ca. 1 mm wide, usually largely concealed by lobes. Lower 1/3 of corolla tube, lobes, and free portions of appendages crimson throughout, interior surface with small yellowish-green spots on lower portion of lobes and adjacent portions of tube, the red pigment extending downward along veins and as spots or short streaks on interior surface between central and lateral petal veins. Stamen filaments becoming free a little below middle of corolla tube. Anthers free, the tips reaching nearly to the level of tips of the corolla lobes of unopened or pressed flowers, the anthers thus being exserted 6-9 mm from mouth of intact corollas with reflexed lobes. Pistil with ovary tapering upward into a distinct, slender style, which bifurcates below the stigmatic surfaces, the stigmas being exserted 2-10 mm beyond mouth of corolla tube, and with the non-placental zones adjacent to the sutures relatively wide, otherwise typical of the section. Both anthers and style branches spiraling in age. Fruit slightly exserted at maturity. Seeds ca. 2 mm long, 0.4 mm wide, prominently winged at one end, wing otherwise narrow but complete.

Gentiana caliculata is endemic to a region comprising the western portion of the Neovolcanic Plateau, from Morelos west to Jalisco, and extending south to the Sierra Madre del Sur in Guerrero (Fig. 10). Here it grows on grassy slopes in the pine-oak zone, flowering from March through June.

Representative specimens examined:

MEXICO: Guerrero: Puerto Rico, *Hinton et al. 14169* (DS, F, GH, MEXU, MICH, NY, POM, UC, US, WTU). Jalisco: Nevado de Colima, *C.G. Pringle 5513* (GH). México: Rincón, *Hinton 11201* (CU, F, GH, ILL, MO, NY, TEX, US, WTU). Michoacán: Sierra Torrecillas, *Hinton et al. 13690* (ENCB, GH, NY, US). Morelos: near Cuernavaca, *C.G. Pringle 7767* (MEXU, VT).

No type specimen for the name *G. caliculata* Lex. has been located, and it is extremely unlikely that any such specimen exists. The only herbarium known to contain specimens collected by La Llave & Lexarza prior to the publication of their *Novorum Vegetabilium Descriptiones* is that of the Conservatoire et Jardin Botanique, Genève (G) (Chaudri et al., 1972; R. McVaugh, personal communication). According to information graciously supplied by Dr. M. Dittrich, *G. caliculata* is not represented among the La Llave & Lexarza collections there.

The only other herbarium known to house La Llave collections is that of the Botanische Staatssammlung, München (M), at which there are four specimens of Mexican gentians collected by La Llave in 1830, after the *Novorum Vegetabilium Descriptiones* had been published. These include one specimen

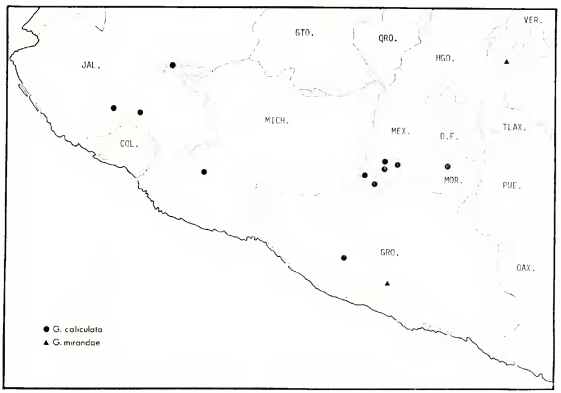

Fig. 10. Documented distribution of *Gentiana caliculata* and *G. mirandae*.

of *Gentiana bicuspidata* and two of *G. spathacea*, all from Angangueo, Michoacán, and one of *Gentianella amarella* (L.) Börner ssp. *hartwegii* (Benth.) J.M. Gillett, from Las Cruces, Distrito Federal. Since none of these specimens was identified to species by La Llave, they do not indicate to what species La Llave & Lexarza applied any of the new specific names published by them.

In the absence of a type specimen for the name *G. caliculata* Lex., whether this species is the same as *G. salpinx* Griseb. has long remained in doubt. Specimens have generally been filed under the name *G. salpinx* in herbaria, but some collectors and curators, including C.G. Pringle and, more recently, E. Matuda and L.B. Smith, have called this species *G. caliculata*.

The type specimen of *G. salpinx* had been labeled "*Gentiana calyculata*" [sic] by Ehrenberg, according to Grisebach (1849) and Bullock (1935), as had the probable replicate in MEXU. Ehrenberg did not indicate whether he had identified these specimens as *G. caliculata* on any basis other than that of Lexarza's (in La Llave & Lexarza, 1824) published description of this species. However, since Ehrenberg was a contemporary of Lexarza's colleague, La Llave, in Mexico, was acquainted with the leading authorities on the Mexican flora at the time, and traveled quite widely in Mexico (Urban, 1897), the possibility that he had some further basis for the identification of

this collection seems not unlikely. Accordingly, I have selected an extant replicate of this Ehrenberg collection as the neotype of *Gentiana caliculata* Lex.

Although Grisebach (1849), Kusnezow (1894), and Bullock (1935) all assumed that *G. caliculata* Lex. and *G. salpinx* Griseb. were different species, each of these authors admitted to being acquainted only with the latter. This assumption appears to have been based almost entirely on Lexarza's (in La Llave & Lexarza, 1824) description of the corolla of *G. caliculata* as being "calyce paulo longior." In all other respects, Lexarza's description of *G. caliculata* appears to constitute an accurate and relatively detailed description of the species subsequently called *G. salpinx*. No other gentianaceous species having red corollas with reflexed lobes, exserted anthers, and the other traits attributed to *G. caliculata* by Lexarza is known from the vicinity of Morelia (formerly Valladolid, latinized Vallisoletum) in Michoacán. Consequently it appears virtually certain that the name *G. caliculata* was applied to the same species as the later name *G. salpinx*, despite the presence of the one discordant element pertaining to the relative lengths of the calyx and corolla in the original description of *G. caliculata*.

A number of authors on pollination ecology, notably Grant & Grant (1968), have observed that certain floral features are commonly associated with hummingbird pollination, especially in North America. Some of these traits, such as the prolonged corolla tube, the abundance of nectar, and the elevation of the ovary above the nectar by a gynophore, prevail throughout sect. *Pneumonanthe* and in much of the genus *Gentiana*. It seems likely, therefore, that other Mexican species of *Gentiana* may occasionally be visited by hummingbirds, although the effectiveness of these birds as pollinators is doubtful. In *G. caliculata*, however, there are a number of floral traits that appear to be specific adaptations to pollination by hummingbirds. These include the red corolla; the reflexed corolla lobes, which eliminate a landing platform that might be used by insects; the exserted anthers and stigmatic lobes; and the deviation of the flowers from the strictly vertical position prevailing in the genus.

The relationships of *G. caliculata* are obscured by the modifications of floral structure involved in the "hummingbird-pollination syndrome." The red corolla, the relatively long style, and the frequent presence of well-developed branches within the cyme are distinct departures from the prevalent morphology of sect. *Pneumonanthe*. The vegetative portions of *G. caliculata*, especially with smaller plants, do, however, resemble those of *G. laevigata*, and the free portions of the corolla appendages are similar to those of certain species in sect. *Pneumonanthe* native to the Pacific Coastal regions of northern North America and northern Asia, such as *G. platypetala* Griseb. and *G. sikokiana* Maxim. These features, along with the bracteation of *G. caliculata* and its relatively short and stout gynophore, indicate that this species is correctly placed in sect. *Pneumonanthe*.

7. GENTIANA MIRANDAE Paray, Bol. Soc. Bot. México 21:15. 1957. Type: MEXICO: Guerrero: faldas del cerro Tlacotepec, Mpio. Tlacotepec, *Paray 2013*, 30 Mar 1956, holotype MEXU! isotype ENCB!, photos HAM! Fig. 11.

Tap root persistent, long and slender (ca. 4.3 mm in diameter at summit and 4 dm long, with 1 fork, in *Pringle 1753*). Stems 1-3, arching or extending nearly horizontally from steep slopes (as seen in Hidalgo) to erect (as described by Paray, 1957), 2-9 dm long, with short, peduncle-like branches from upper 1 or 2 nodes, the longer stems also with short leafy branches from lower nodes, minutely papillose-puberulent in lines near nodes, otherwise glabrous, often suffused with purple. Leaves medium to dark green, sometimes suffused with purple, lanceolate to ovate, lower ones obtuse to acute, upper ones acute to acuminate at apex, rounded at base, those between the middle of the stem and base of inflorescence largest, 3-8 cm long and 1.8-3.5 times as long as wide, with 3 or 5 prominent veins. Lower leaves gradually smaller, the lowest mere scales. Leaf margins minutely denticulate, very narrowly revolute except sometimes near base. Upper 2-5 internodes 2-7 cm long, lower ones gradually shorter. Flowers occasionally solitary, usually in terminal, sometimes imperfectly developed, cymes of 3-5, and sometimes also solitary or paired at ends of short branches from the first 1-6 nodes below the terminal cymes, the 2 flowers borne on opposite cyme branches or terminating the same branch reaching anthesis asynchronously. Each flower subtended by a pair of linear to lanceolate bracts 1-3.5 cm long. Calyx tube uncleft, 7.5-20 mm long, 5-ridged, glabrous. Calyx lobes erect, linear to oblong, 6-14 mm long, 1-2 mm wide, narrowly carinate, abruptly acuminate, with margins minutely denticulate proximally, entire distally. Corolla tube cylindric, 4.5-7.5 cm long, 8-12 mm in diameter. Corolla lobes erect to slightly divergent, ovate-triangular, 4-6 mm long and about as wide as long, entire, acute to acuminate, the sinus adjacent to outer edge of each lobe slightly lower than the other. Free portions of corolla appendages obliquely triangular, ca. 2 mm long, acute, entire or sparingly erose. Corolla tube above summit of calyx tube (except sometimes for lowest 1-10 mm), along with lobes and free portions of appendages yellow in bud, orange-red at anthesis, becoming scarlet, then purplish brick-red when the stigma is receptive. Corolla tube not striped on interior surface. Stamen filaments becoming free at 0.33-0.38 times length of corolla tube; free portions very slender, elevating anthers so that their tips approach or slightly exceed the level of the tips of corolla lobes. Anthers ca. 3.5 mm long, not cohering. Ovary 1.8-3 cm long when stigma is receptive, elevated by a gynophore about the same length. Style deeply 2-cleft, the divisions slender, continuing to elongate and coiling after anthesis (the flowers being strongly protandrous), the stigmatic surfaces exserted beyond tips of corolla lobes. Fruits and seeds not seen.

Gentiana mirandae is known only from the type collection (from Guerrero) and from the three collections from one Hidalgo locality cited below,

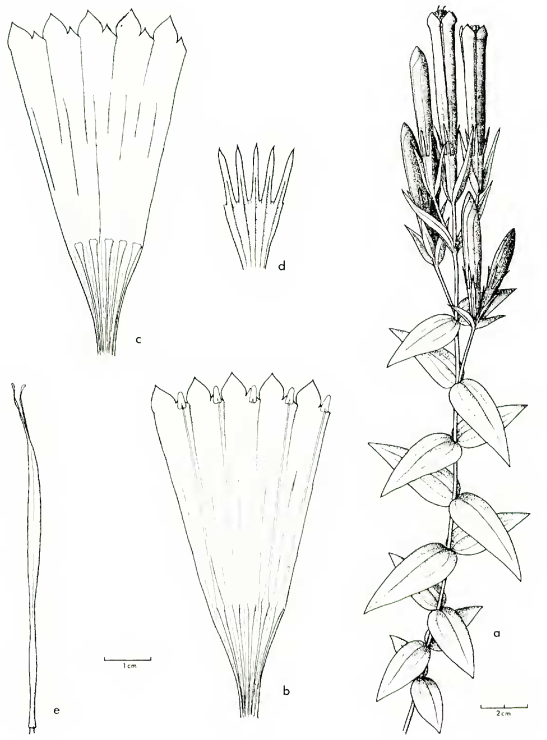

Fig. 11. *Gentiana mirandae*. a, flowering stem; b-c, interior surfaces of corollas, with stamens present (b) and stamens removed (c), and d, calyx, slit longitudinally and pressed; e, pistil.

which were identified during the present study (Fig. 10). The type collection was made in openings on wooded slopes with *Pinus* and *Alnus* dominant, at 2200-2500 m altitude, and those from Hidalgo on a steep, rocky roadside bank in *Pinus-Alnus* woods about 2100 m. All four collections were made in March, at which time the plants were in full bloom.

Additional specimens examined:

MEXICO: Hidalgo: El Estribo, carretera Tulancingo-Tenango, km 42, *Gimate L. 509* (ENCB); carretera Tulancingo-Tenango, km 44, *Gimate L. 542* (ENCB); 18.4 km by road NE of Metepec on road to Tenango de Doria, *J.S. Pringle 1753* (HAM, MEXU, pollen SPN).

Like *G. caliculata*, *G. mirandae* appears to be adapted to pollination by hummingbirds, as it, too, has long-tubed, red corollas and exserted anthers and stigmatic lobes. Its corolla lobes, although erect rather than reflexed, likewise fail to provide a landing platform. The branching pattern of *G. mirandae*, its corolla shape and color, and its elongate gynophore, which is unique among species in sect. *Pneumonanthe*, give this species an aspect similar to that of certain species in the Asiatic sect. *Stenogyne* Franch. The carpels of *G. mirandae*, however, have seven vascular bundles each, with the ovules being distributed over much of the interior surface, and thus conform to the pattern of ovarian anatomy reported for sect. *Pneumonanthe* by Lindsey (1940) and differ from that of sect. *Stenogyne*.

The disjunction in the known range of *G. mirandae* is not readily explicable, since pine-alder forests, which constitute the habitat of *G. mirandae* as far as is known, occur extensively between the stations of this species in Guerrero and Hidalgo. Although additional populations may be found in the future, it seems certain that *G. mirandae* is genuinely rare and widely disjunct in its occurrence. Some differentiation may exist between the Guerrero and Hidalgo populations, as indicated by Paray's (1957) description of the Guerrero plants as being erect and as having larger flowers than those seen in Hidalgo. Specimens from both regions, however, are so similar in details of leaf, calyx, and corolla morphology that their taxonomic separation would be unwarranted.

Interspecific hybrids

Although, in view of the extensive interfertility among species of sect. *Pneumonanthe*, it seems unlikely that the Mexican and Central American species are separated by barriers of incompatibility, hybridization among these species seems to be extremely rare. Some species are ecologically isolated from others; *G. ovatiloba*, for example, being virtually restricted to alpine habitats, rarely occurs in proximity to species growing at lower elevations. Genetic exchange among the species of the pine-oak of the Mexican mountains appears to be minimized by the tendency of these species to occur in small, scattered populations and by the fragmented distribution of the habitat itself.

Specimens cited above as examples of variation within one species in the direction of its nearest Mexican relative should probably not be considered to represent the results of interspecific hybridization. Some of these specimens may simply represent intraspecific variability that by chance happens to result in similarity to a related species in one or two traits. Others may represent patristically intermediate populations persisting in isolated, relatively stable habitats as remnants of ancestral complexes that existed before the differentiation of present-day species was complete.

True hybridization between well-differentiated species of *Gentiana* in Mexico appears to be represented only by a series of collections by L. Paray, from the vicinity of Contreras, Distrito Federal, mapped in Fig. 6g. *Paray 1247* (ENCB) and two of the stems in *Paray 1248* (ENCB) are typical of *G. spathacea*, *Paray 1249* (ENCB), from the same area, represents *G. bicuspidata*, with some of the specimens on this sheet showing evidence of hybridization. *Paray 3451* (DS, ENCB, MEXU, MICH, MSC) and the remaining components of *Paray 1248* are collections of evident hybrids between *G. bicuspidata* and *G. spathacea*, as Paray suspected in the case of *3451* (in sched.). These specimens have decumbent to ascending stems 2-4 dm long, some bearing small, leafy branches or tufts in some of the leaf axils. The leaves are ovate, the larger ones 2.2-4.5 cm long, 2.5-3 times as long as wide, with the apices of the lower leaves obtuse, those of the upper leaves varying from obtuse to acute. The flowers are borne in small terminal clusters and singly at the ends of peduncle-like branches up to 30 mm long, the branches usually in pairs, but one member of the pair sometimes terminating in an abortive flower only. The flowers are individually subtended by ovate bracts 12-20 mm long. The calyces are uncleft, with broadly linear to ovate-oblong lobes 4-7 mm long. Corolla length ranges from 2.7-3 cm on one stem to ca. 4 cm on another. The corolla lobes are orbicular or nearly so, 4-6 mm long, obtuse or minutely apiculate. The free portions of the appendages are bicuspidate. *Paray 367* (ENCB), from the Sierra de Las Cruces, about 10 km to the west of Contreras, consists of highly similar plants that are probably of the same origin.

Unconfirmed Report

The range of *Gentiana affinis* Griseb. in Hook., Fl. Bor.-Am. 2:56. "1840" [1837] was said to extend from British Columbia and Alberta south to California, Arizona, and northern Mexico by Hitchcock (1959). No specimens were located during the present study that would substantiate this report of *G. affinis* from Mexico. There are specimens of *G. affinis* (as *G. interrupta*, a taxonomically insignificant variant of this species) and *G. parryi* A. Gray in F, collected by Brother G. Arsène et al. in 1926, that bear labels with the printed heading "Plantes du Mexique." The handwritten locality data, "Las Vegas," however, doubtless refer to Las Vegas, San Miguel County, New Mexico, where Arsène is known to have collected plants in 1926 (Ewan, 1950), rather than to a Mexican locality.

Kearney et al. (1942) have reported *G. affinis* (as *G. bigelowii*, another minor variant) occurring as far south as Cochise and Pima counties in southeastern Arizona. *Gentiana affinis*, therefore, might be expected in the Sierra de San Bernardino and the Sierra de San Luís in adjacent northeastern Sonora.

Detailed descriptions of *G. affinis*, accompanied by illustrations, have been published by Hitchcock (1959) and by Gillett (1963).

ACKNOWLEDGMENTS

I express my sincere thanks to: the curators and staff of the herbaria listed in the introduction of this paper, for the loan of specimens or for their hospitality and cooperation during my visits to their institutions; to those at B, K, M, and OXF, for supplying photographs of nomenclaturally important specimens; to the Consejo Nacional de Ciencia y Tecnología, for permission to collect specimens of *Gentiana* in Mexico; to Drs. John M. Gillett and Rogers McVaugh, for their reviews of a preliminary version of the manuscript, and for valuable information and suggestions; to Dr. Thomas Duncan, for his cooperation and assistance with field work; and to the Board of the Royal Botanical Gardens, for its contributions to the support of the research and to the publication of this paper.

REFERENCES

BENTHAM, G. 1839-1857. Plantae Hartwegianae. London: Gulielmus Pamplin. 2 sections in 23 signatures. (*Gentiana* in 4th signature of section 1, 1840.)

BRIQUET, J. 1931. Decades plantarum novarum vel minus cognitarum: Series altera, Decades 26-28. Candollea 4:317-352.

BULLOCK, A. A. 1935. *Gentiana salpinx* Griseb. Hooker's Icon. Pl. 33:tab. 3299.

CHAUDRI, M. N., I. H. VEGTER, and C. M. DE WAL. 1972. Index Herbariorum. Part II(3): Collectors I—L. Regnum Veg. 86:i-xxii, 297-473.

DON, G. 1831-1838. A General History of the Dichlamydeous Plants . . . . London: J. & G. Rivington et al. 4 vols. (Gentianaceae in vol. 4(1), 1837.)

EWAN, J. 1950. Rocky Mountain Naturalists. Denver: University of Denver Press, xiv + 358 pp.

FABRIS, H. A. 1960. El género *Gentianella* en Ecuador. Bol. Soc. Argent. Bot. 8:160-192.

FLORES MATA, G., J. JIMENEZ LOPEZ, X. MADRIGAL SANCHES, F. MONCAYO RUIZ, and F. TAKAKI TAKAKI. 1971. Mapa de Tipos de Vegetación de la Republica Mexicana. México, D.F.: Secretaria de Recursos Hidráulicos, Subsecretaria de Planeación, Dirección General de Estudios, Dirección de Agrologia. 1 map.

GAUDIN, "I." [J.F.G.P.]. 1828-1833. Flora Helvetica . . . Zurich: Orelli, Fuesslin et Socii. 7 vols. (*Gentiana* in vol. 2. 1828.)

GILG, E. 1895. Gentianaceae. *In*: Engler, [H.G.] A., & K. [A.E.] Prantl. Die natürlichen Pflanzenfamilien . . . Leipzig: Verlag von Wilhelm Englemann. 4(2):50-108.

GILLETT, J. M. 1957. A revision of the North American species of *Gentianella* Moench. Ann. Missouri Bot. Gard. 44:195-269.

———. 1963. The Gentians of Canada, Alaska and Greenland. Res. Branch, Canada Dept. Agric. Publ. 1180. 99 pp.

GRANT, K. A. and V. GRANT. 1968. Hummingbirds and their Flowers. New York: Columbia University Press. viii + 115 pp.

GRAY, A. 1886. Synoptical Flora of North America [vols. 1(2) & 2(1)]: The Gamopetalae, ed. 2. Washington: Smithsonian Institution. 2 parts.

GRISEBACH, A.H.R. "1839" [1838]. Genera et Species Gentianearum . . . Stuttgart & Tübingen: J. G. Cotta. viii + 364 pp.

———. 1845. Gentianaceae. *In*: Candolle, A.P. de, & A. de Candolle, eds. Prodromus Systematis Naturalis Regni Vegetabilis . . . Paris: Fortin, Masson et Socii. 9:38-141.

———. 1849. Gentianeae Juss. *In*: Klotzsch, J.F. Beiträge zu einer Flora der Aequinoctial-Gegenden der neuen Welt. Linnaea 22:32-46.

HITCHCOCK, C. L. 1959. *Gentiana* L. Gentian. *In*: Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. Vascular Plants of the Pacific Northwest. Univ. Wash. Publ. Biol. 17(4):63-73.

HOLMGREN, P. K. and W. KEUKEN. 1974. Index Herbariorum. Part I: The herbaria of the world, ed. 6. Regnum Veg. 92. vii + 397 pp.

HUMBOLDT, [F.H.]A. von, A.[J.] BONPLAND, and C. S. KUNTH. 1815-"1823" [1-1825]. Voyage aux Regions Equinoctiales du Nouveau Continent, Fait en 1799-1804. Sixième Partie. Botanique. Sect. 3. Nova Genera et Species Plantarum . . . . Paris: Libraria Graeco-Latino-Germanica. 7 vols. in 36 parts. (*Gentiana* spp. described in vol. 3(10). 1819; note on the name *G. plicata* in vol. 5(23). 1823.)

JONES, M. E. 1908. New species and notes. Contr. W. Bot. 12:1-81.

KEARNEY, T. H., T. H. PEEBLES, and collaborators. 1942. Flowering Plants and Ferns of Arizona. U.S.D.A. Misc. Publ. no. 423. 1069 pp. + 30 pl.

KUSNEZOW, N. J. 1894. Podrod *Eugentiana* Kusnez. poda *Gentiana* Tournefort. Sistematicheskaja, morfologicheskaja i geograficheskaja obrabotka. Trudy S.-Peterburgsk. Obshch. Estestvoisp., Otd. Bot. 24:2nd independently paged part. v + 531 pp. + 1 pl. + 4 maps + 7 tables.

———. 1895. *Gentiana* Tournef. *In*: Engler, [H.G.]A., & K.[A.E.] Prantl. Die natürlichen Pflanzenfamilien . . . . Leipzig: Verlag von Wilhelm Engelmann. 4(2):80-86.

LA LLAVE, P., and J. LEXARZA. 1824-1825. Novorum Vegetabilium Descriptiones . . . . México: Martin Rivera. 2 vols. (*Gentiana* in vol. 1. 1824.)

LEOPOLD, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507-518.

LINDSEY, A. A. 1940. Floral anatomy in the Gentianaceae. Amer. J. Bot. 27:640-652.

LOEVE, A. and D. LOEVE. 1975. The Spanish gentians. Anales Inst. Bot. Cavanilles 32:221-232.

MARTENS, M. and H. GALEOTTI. 1842-1845. Enumeratio synoptica plantarum phanerogamarum ab Henrico Galeotti in regionibus Mexicanis collectarum. Bull. Acad. Roy. Sci. Bruxelles 9(1):526-544; 9(2):32-47, 227-249, 372-393; 10(1):110-146, 208-224, 341-361; 10(2):31-52, 178-200, 302-321; 11(1):121-137, 227-243, 365-376; 12(1):129-149; 12(2):15-36, 257-278. (*Gentiana* in vol. 11(1). 1844.)

MASON, C. T., JR. and H. H. ILTIS. "1965" [1966]. Preliminary reports on the flora of Wisconsin No. 53. Gentianaceae and Menyanthaceae—Gentian and Buckbean families. Trans. Wisconsin Acad. Sci. 54:295-329.

McVAUGH, R. 1945. The jatrophas of Cervantes and of the Sessé & Mociño herbarium. Bull. Torrey Bot. Club 72:31-41.

MILLER, H. S. 1970. The herbarium of Aylmer Bourke Lambert: notes on its acquisition, dispersal, and present whereabouts. Taxon 19:489-553.

NILSSON, S. 1967. Pollen morphological studies in the Gentianaceae—Gentianinae. Grana Palynol. 7:46-143.

PARAY, L. 1957. *Gentiana Miramdae* y *Corcopsis lucida*, sp. nov. de México. Bol. Soc. Bot. México 21:15-19.

PRINGLE, J. S. In press. Sectional and subgeneric names in *Gentiana* (Gentianaceae). Sida.

RAISZ, E. 1964. Landforms of Mexico, ed. 2. Cambridge, Massachusetts: the author. 1 map.

RORK, C. L. 1949. Cytological studies in the Gentianaceae. Amer. J. Bot. 36:687-703.

SMITH, H. 1936. Gentianaceae. *In*: Handel-Mazetti, H. von. Symbolae Sinicae: Botanische Ergibnisse der Expedition der Akademie der Wissenschaften in Wien nach Südwest-China, 1914-1918. Wien: Verlag von Julius Springer. 7:948-988.

———. 1967. Appendix. *In*: Nilsson, S. (1967), q.v., pp. 144-145.

STAFLEU, F. A. 1967. Taxonomic Literature: a Selective Guide to Botanical Publications with Dates, Commentaries and Types. Regnum Veg. vol. 52. xx + 556 pp.

STANDLEY, P. C. 1920-1926. Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb. vol. 23. 5 parts. (History of botanical exploration in Mexico in part 1. 1920.)

——— and J. A. STEYERMARK. 1944. Studies of Central American plants—IV. Publ. Field Mus. Nat. Hist., Bot. Ser. 23:31-109.

——— and L. O. WILLIAMS. 1969. Flora of Guatemala, part VIII, number 4: Contortae. Fieldiana, Bot. 24:263-474.
STEYERMARK, J. A. 1950. Flora of Guatemala. Ecology 31:368-372.
TOYOKUNI, H. 1963. Conspectus Gentianacearum Japonicarum: a general view of the Gentianaceae indigenous to Japan. J. Fac. Sci. Hokkaido Imp. Univ., Ser. 5, Bot. 7:137-259, pl. I-IV.
TUTIN, T. G. 1972. *Gentiana* L. *In*: Tutin, T. G., et al., eds. Flora Europaea. Cambridge, U.K.: University Press. 3:59-63.
URBAN, I. 1897. Biographische Skizzen. V. 6. Carl August Ehrenberg (1801-1849). Bot. Jahrb. Syst. 24(Beibl. 58):1-13.
WAGENITZ, G. 1964. Reihe Gentianales (Contortae, Loganiales, Apocynales). *In*: Melchior, H., ed. Engler's Syllabus der Pflanzenfamilien . . . , ed. 12. Berlin: Gebrüder Borntrager. 2:405-424.
WEAVER, R. E., JR. and L. RUEDENBERG. 1975. Cytotaxonomic notes on some Gentianaceae. J. Arnold Arbor. 56:211-219.
WILLIAMS, L. O. 1968. Tropical American plants, IX. Fieldiana, Bot. 31:401-425.